THE

NEW PHYTOLOGIST,

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A.

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE,

CONSULTATION WITH THE STAFF OF THE CAMBRIDGE BOTANY SCHOOL.

ASSISTANT-EDITOR:

F. CAVERS, D.Sc.

VOLUME XII.

PP. VIII. AND 368.

WITH SIX PLATES AND NUMEROUS FIGURES IN THE TEXT.

LONDON 1913

WILLIAM WESLEY & SON

28 ESSEX STREET, STRAND.

INDEX OF SUBJECTS.

Page

INDEX OF AUTHORS.

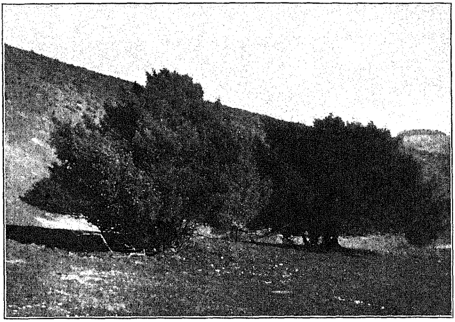


Fig. 1.

Fig. 2.

LINDMAN.—PLANTS SUPPRESSED BY OTHER PLANTS.

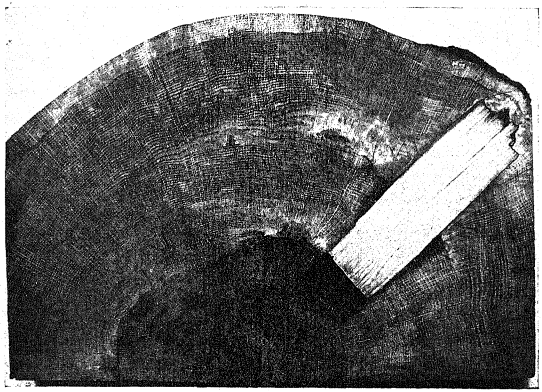


Fig. 1.

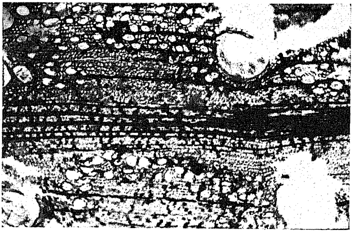
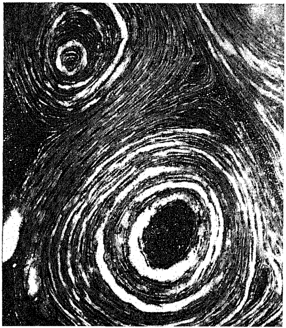
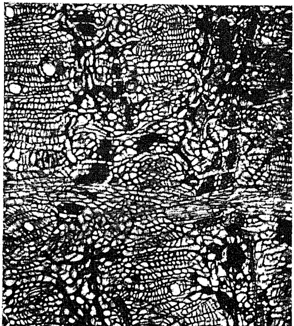


Fig. 2.





THE

NEW PHYTOLOGIST.

VOL. XII, No. I. JANUARY, 1913.

[PUBLISHED JAN. 31ST, 1913].

SOME CASES OF PLANTS SUPPRESSED BY OTHER PLANTS.

BY C. A. M. LINDMAN (Stockholm).

[WITH PLATE I AND ONE FIGURE IN THE TEXT].

I.

EVERY botanist is well acquainted with the fact that certain plants of considerable size and dense growth exercise an influence disadvantageous to much of the accompanying flora: the deep shade cast by such plants prevents many species from attaining a normal development and finally kills them. The common nettle for instance, *Urtica dioica*, is able to suppress other plants entirely, so that if a large *Urtica*-group is cut away, there will be seen no other vegetation on the central parts of the area occupied by the nettles, the soil being quite bare. The International Phytogeographical Excursion in the British Isles (1911) visited the woods in the neighbourhood of Honley, Yorks., and the party had the opportunity of admiring the gigantic form of *Pteridium aquilinum*, widely distributed in shady woods on the slate, and differing from the dwarf form on siliceous grasslands.[1] *Pteridium* also is a plant which grows so densely that it may exclude all herbs and grasses. I have seen the same species in South Brazil, where it forms enormous thickets very much higher than in Britain (leaves are met with 6 to 7 m. long; at Honley I saw leaves 2 m. long.) In Brazil, however, this fern grows abundantly, chiefly in sunny places where the forest has been destroyed[2], and consequently it has there not quite the same biotic influence as in the British

[1] See T. W. Woodhead, "Ecology of Woodland Plants." Journ. Linn. Soc., Bot., 1906, p. 368; also A. G. Tansley, "Types of British Vegetation," 1911, Plate I.

[2] Mentioned by P. W. Lund in 1835, and E. Warming in "Lagoa Santa," 1892, &c.

woods just mentioned, where it belongs to the shade ground vegetation.

A well-known example of the same kind is the suppressing effect which the beech (*Fagus silvatica*) and the spruce (*Picea*), both of which constitute very dark forests, exercise on the oak. In Germany and in South Sweden the oak, *Quercus robur*, eventually yields to the beech; and in Central Sweden (*e.g.* at Stockholm) isolated old and nearly ruined oaks are met with in the pure spruce woods, where, for want of daylight, no oak seedlings are nowadays seen.

There is, however, another European forest-tree, the shade of which is still more intense than that of the beech. This is the yew (*Taxus*), of which the largest and purest wood in the British Isles, the famous wood of Kingley Vale (Sussex), was shown to the foreign members of the International Excursion, and caused their enthusiastic admiration. In this yew wood the ground was to a great extent entirely bare,[1] without any vegetation, phænogamous or cryptogamic, consisting only of a dark brown earth, and never reached by any sun glimpse. There is evidently in the British flora no species able to settle and form a ground vegetation in darkness like this. In the tropics, *e.g.*, South Brazil, the darkest woods and groves never lack a dense ground vegetation of miniature trees, ferns, and a few herbs.[2]

Plate I, Fig. 1 shows two individuals of *Taxus* at the margin of the large yew wood at Kingley Vale; one of these (to the left) is seen behind a large juniper, in the faint shade of which the yew has germinated. Later on, the juniper will be hidden, suffocated and killed by its neighbour, as has already happened with the junipers beneath the larger yew to the right. There is hardly a stronger contrast in British nature, in regard to the available light, than that between the black interior of the pure, dense yew wood and the complete exposure on the bright southern slope of a chalk down.

II.

I shall now call attention to a herbaceous plant, which, even when present as isolated individuals, is able to suppress its nearest neighbours by the shade of its leaves, together with the direct contact and pressure. This is *Hypochœris maculata*. In Great Britain it is recorded from the chalk and limestone; on similar habitats in Sweden it generally occurs in a dwarf form with small

[1] See also A. G. Tansley, "Types of British Vegetation," p. 170.

[2] I have endeavoured to sketch this in the book, "Vegetation in Rio Grande do Sul," 1900, pp. 130, 163.

deeply cut leaves. But on the siliceous and granitic ground of Central Sweden it grows very tall and produces radical leaves up to 20 cm. long and 8 cm. broad. On dry hill-sides and on the borders of pine woods, in close short pasture on sandy or loamy drifts (old ground moraines), this species is sometimes numerous, the large radical leaves all horizontally expanded, and the large flat rosette pressed to the ground. It is evident that all small and weak plants beneath such a rosette would be pressed down and kept in obscurity during 4—5 months.

The herbaceous vegetation of these localities is poor, more rarely a fairly good pasture, consisting chiefly of *Potentilla erecta*, *P. verna*, *Veronica officinalis*, *Campanula rotundifolia* (a tiny form), *Leontodon autumnalis*, *Luzula campestris*, *L. multiflora*, *Agrostis vulgaris*, *Festuca ovina*, &c. Although the rosette leaves of *Hypochœris maculata* are not very firm, all the plants mentioned succumb to the pressure and the shade, and it is curious to see how below a *Hypochœris*-rosette there are only tiny, etiolated shoots or bare soil. Several plants, however, save themselves by a long creeping stem, which does not suffer at all when the base is covered, e.g., *Potentilla erecta* and *Veronica officinalis*, and others (*Campanula rotundifolia*) by short runners or stolons; but many herbs and all mosses and lichens are suppressed by the large-leaved *Hypochœris*. In somewhat shady places where *Dactylis glomerata*, *Melampyrum nemorosum*, *Ranunculus acer*, *R. polyanthemus*, *Silene nutans*, *Galium boreale*, *Festuca elatior*, *F. rubra*, *Trifolium medium*, &c., are growing (the examples are chosen from the vicinity of Stockholm), the basal leaves of *Hypochœris* are not able to do any harm, as they are forced into an upright position.

III.

One of the most striking examples of a herbaceous plant possessing an irresistible power to force away and displace the accompanying plants in the same association by means of strong growth and firm stiff leaves, is *Juncus squarrosus*. This species was seen abundantly on high-lying dry plateaux and slopes in northern England and Scotland during the International Phytogeographical Excursion, 1911.

Many of the members of the Excursion will remember it. On the grit grassland at the higher levels of Crossfell in Westmoreland (Text-Fig. 1), on the immense, slightly inclined slopes of Ben Lawers (Plate I, Fig. 2), and in several other places.

The British form met with in the dry, hot summer of 1911 was

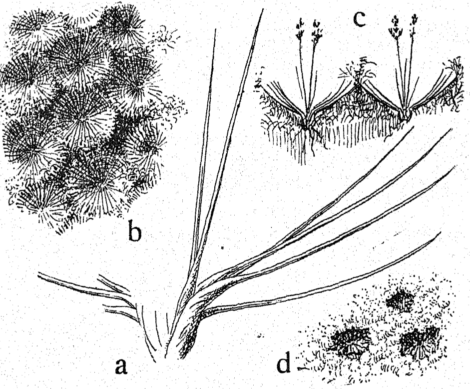


Fig. 1. *Juncus squarrosus* (Crossfell, Aug. 13th). *a*, some of the basal leaves (about half natural size); *b*, a group of rosettes seen from above, the interspaces filled up by *Agrostis vulgaris*; *c*, two individuals in vertical section (schematic); *d*, some rosettes in a *Sphagnum* bed nearly shut up,

very short and coarsely growing, the rosette leaves only 10—12 cm. long. The species occasionally produces leaves 20—30 cm. long. As it was observed rather late in the year (August), and with ripe fruits or nearly so, its most peculiar feature, the spreading leaves, was very distinctly developed.

In fact, this peculiar manner of growth attracted the attention of many of the party. Having made some notes on the subject and some schematic drawings, I asked my companions whether there was any record of this matter. Nobody had any knowledge of such observations, nor have I later found anything published on the singular behaviour of *Juncus squarrosus* to the surrounding vegetation. I therefore now give a short account of the action of this plant in suppressing other herbs and grasses of its habitat.

Where *Juncus squarrosus* occurs abundantly, it seems to cover the ground entirely (see Plate I, Fig. 2). It occupies great areas, and I saw places where I could walk a hundred yards in a straight line without seeing any interruption in the apparently pure "Juncetum squarrosi."

At the same time the plant differs from its neighbours by forming, not a smooth continuous lawn or carpet, but a rough pasture, where each individual rosette (more correctly each plant

composed sympodially of several axillary rosettes) has the shape of a shallow cup or of a bird's nest (Text-Fig. 1, *b*, *c*), in the centre of which the leafless stem arises. A single individual (*viz.*, the flowering stem, sometimes two or three together, with the—simple or compound—rosette) has generally about twenty green leaves, or even twice as many, besides the dead brownish ones from the preceding year. All these leaves are bent outwards at the very base (Fig. 1, *a*), as soon as they become full-grown. In June and July there are still young, soft leaves in the middle, standing up close to the inflorescence; but in August they are all spreading rigidly outwards.[1] They spread at an angle of 40—90° to the perpendicular and force away all the surrounding herbs and grasses, except the adjoining rosettes of the same species, for every time *Juncus squarrosus* was seen in great numbers and the rosettes adjoined each other, they were all of the normal size (a diameter of about 1 dm.), and the distance from centre to centre is the same as the diameter of a rosette (Fig. 1, *b*).

Owing to the considerable number and thickness of the blades, the bottom and sides of the "cup" or "nest" are quite impermeable to the shoots of other plants.

In dense colonies of *J. squarrosus* there will be very little space left for other herbaceous plants. On Crossfell the commonest plant accompanying *J. squarrosus* was *Agrostis vulgaris* (*A. tenuis* Sibth. ?), a tender form with narrow leaves. This plant has but little ability to resist the pressure of the *Juncus*, and where the latter was growing densely, the *Agrostis* appeared as thin vertical layers, jammed in between the rosettes of the *Juncus* (Fig. 1, *b*, *c*) and scarcely overtopping its leaf points. As the *Juncus* leaves partly keep green and fresh in the winter and do not lose their form and firmness after withering, the *Agrostis* has no chance to recover its lost position. In fact, below and between the *Juncus* rosettes there is a soft mass of withered *Agrostis* leaves, but this plant now produces numerous axillary shoots higher up on the stem than usual. It is thus evident that *Juncus squarrosus* would fail to get air and light enough, were it not able to keep its rosette open by means of the rigidly spreading leaves.

Other species which grow with *J. squarrosus* on Crossfell, and are caught and suppressed in the same way as *Agrostis vulgaris*, are *Deschampsia flexuosa*, *Festuca ovina*, *Galium saxatile*, *Vaccinium*

[1] The anatomical structure is figured in Raunkiaer's "De Danske Blomsterplanters Naturalhistorie," **1**, 1895—99, p. 407, fig. 194, D; and Kirchner, Loew and Schroeter's "Lebensgesch. d. Blütenpflanzen Mitteleuropas," Lief. 10, 1909, p. 104, fig. 61.

myrtillus (the dwarf form of the hills in northern England), *Polytrichum* sp. (without sporangia), *Dicranum* sp., a few other mosses, and *Cladonia rangiferina.* More rarely this was the case with *Nardus stricta.* On Ben Lawers even the predominant, firm and rigid *Alchemilla alpina* was shut up and flattened, where the rosettes of *J. squarrosus* occurred densely (see Plate I, Fig. 2).

Only in *Sphagnum* does *Juncus squarrosus* seem to succumb. I once saw these two together (Crossfell); the *Juncus* was sunk rather deeply in the wet *Sphagnum* bed, and this grew freely over the leaf points of the rosettes. Consequently the *Sphagnum* was able to shut up the rosettes (as seen in Fig. 1, *d*), and on account of the peculiar consistence and nearly amorphous growth of the moss bed, it is not likely that it would be forced back by the spreading *Juncus* leaves.

Of herbaceous plants there are indeed very few that constitute such an effective biotic factor as *J. squarrosus*, unless they have strong mechanical resources for the struggle against plants of the same size. A similar effect we may of course expect in the case of woody plants, which in fact very often become predominant in various associations other than scrub and woodland. In the British Isles there are good examples in *Ulex europæus* and *U. Gallii* on heaths and pastures, *Vaccinium myrtillus*—together with *Rubus chamæmorus*—on the "peat hags" of the Pennines, &c. As regards *Juncus squarrosus*, there is no doubt that, although it is very much eaten by sheep, it will proceed in its conquest of the upland pastures, as long as the climatic conditions are favourable.

Description of the Photographs on Plate I, Illustrating Prof. Lindman's Paper on "Plants Suppressed by other Plants."

Fig. 1. Yews and Junipers at Kingley Vale, illustrating the suppression of Juniper by Yew. Phot. W. B. Crump, 1911.

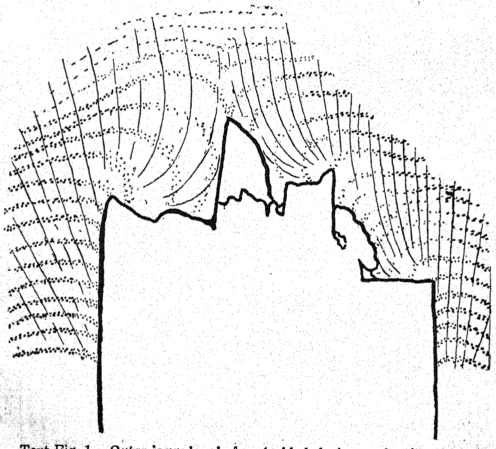
Fig. 2. *Juncus squarrosus* on Ben Lawers: several plants forming a pure clump in association of *Alchemilla alpina*. Phot. J. Massart, 1911.

SOME OBSERVATIONS ON WOUND HEALING IN A SPECIES OF OAK.

By A. V. Duthie.

[With Plate II and Three Text-Figs.]

THE slab of oak under consideration was sent to Professor Seward by Mr. Sindall of Cambridge. The wood is stated to be Austrian oak and from its general appearance and structure probably belongs to the species *Q. pedunculata*. Assuming that a single ring was produced each year the trunk must have been 160 years old when felled, with a diameter of 37cm. The ten outer rings, which belong to the sap-wood, are much lighter in colour than the heart-wood, and the limit between the two is made still more evident to the naked eye by a dark brown border due to the presence of tanniniferous contents in the cells of the wood-parenchyma and medullary rays (Plate II, Figs. 1 and 2).



Text-Fig. 1. Outer jagged end of embedded deal peg showing occluding callus layers.

The tree from which the slab was sawn received numerous wounds at different periods of its growth. The most striking of these is due to the insertion of a deal peg when the tree was 112

years old (Plate II, Fig. 1). The wood was morticed out to the depth of about 13 cm., and the peg, which is $6\frac{1}{2}$ cm. thick and 22 cm. long, was driven in, leaving about 13 cm. projecting from the wound. This projecting portion was completely covered over in 38 years. The effect of the injury is observable in the widening of the annual rings to a lateral distance of over 5 cm. from the wound. The average breadth of the rings formed immediately before the injury is under 3 mm., the greatest breadth (12 mm.) is reached in the second year after wounding. From this point the breadth of the successively formed rings of wood decreases, until after 9 years from the injury the breadth of about 3 mm. is once more attained.

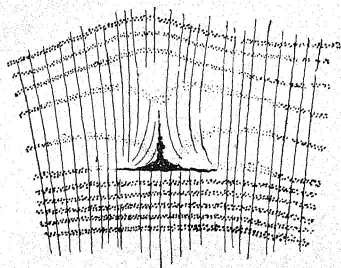
As the callus lips arch over the jagged end of the deal peg they broaden once more (Fig. 1), pushing into every crevice and coming into close contact with its irregular surface. A considerable amount of cortical tissue was formed in the callus-cushions before their coalescence; this is easily recognised by the brownish appearance of the tissues lying next to the peg and the interspersed groups of sclerotic cells. Owing to the pressure exerted by the fusing callus lips the arrangement of tissues is in this region much confused, groups of bark and wood elements being intermingled.

The callus wood which has closed over the end of the embedded peg shows in a very marked degree the phenomenon known as "speckled" or "curled" grain.[1] The large medullary rays as seen in tangential section do not exhibit the usual narrow elliptical form but are broadly oblong, triangular or circular in outline; while the course of the wood elements is much twisted (Plate II, Fig. 3). This peculiarity of structure is due in part to the jagged nature of the surface covered over by the callus and in part to the formation of adventitious buds, two of which are shown in transverse section in Plate II, Fig. 3.

In six of the remaining seven wounds exhibited by the specimen the outer tissues alone have perished and healing by occlusion has resulted. The injuries occurred in the 50th, 61st, 63rd and 113th years of growth. The area of wood laid bare by these wounds varied in extent and the healing process occupied from two to five years according to the extent of the injury. In the largest wounds examined the exposed wood has undergone considerable decomposition, and fungus spores and mycelial threads were noticed. In other cases the exposed wood is perfectly sound and has been effectually protected against decay by the formation of tyloses and the impregnation of the walls with tannin.

[1] Frank. Krankheiten der Pflanzen, I, p. 80.

Owing to the reduction of bark-pressure in the region of these injuries, broad callus lips have been produced which have arched over the exposed surface and finally coalesced (Text-fig. 2). As the exposed cambium perished completely there is no cohesion between the callus-tissue and the old wood. In several wounds a thin layer of entrapped cork was found between the callus cushions, and the remains of cortex and bast, which developed on their rounded surfaces before these met and fused, can be seen distinctly. Particularly noticeable are the groups of sclerotic cells which appear as



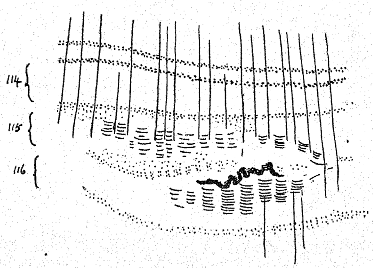
Text-fig. 2. Transverse section of part of oak-stem showing wound which has healed completely in two years.

more or less translucent brown specks embedded in masses of thick-walled cells with tanniniferous contents. As healing proceeded the callus lips pressed closely against each other, displacing the outer tissues, until finally the cambium layers came into contact and thickening proceeded normally. Even after the wounds have healed completely the effect of the injury still appears in the broadening of the wood ring immediately following.

All the wounds considered thus far have exhibited the usual method of healing by the formation of callus cushions from the living tissues at the edges of the wounded area. The remaining injury, which lies about 5 cm. to the right of the peg, has apparently healed in a somewhat different manner (Text-fig. 3).

The broadening of the 114th ring is due to the lateral influence of a rind gall a little to the left, which is not shown in the diagram. The summer wood of each of the two succeeding rings passes into a tissue which at first sight suggests a portion of enclosed phloem. This abnormal tissue appears to the naked eye as a series of undulations each bordered by a darker line. In places the alternation of

lighter and darker striations is extremely regular as may be seen to the right of the diagram (Text-fig. 4.) Fig. 4 is a photomicrograph of part of a transverse section cut through this abnormal region. It shows regularly-arranged groups of strongly-thickened fibres which resemble closely those formed in the normal bast and are in contact with vertical rows of crystal-containing parenchymatous cells. Alternating with these bands of fibre-groups are zones consisting of thick-walled pitted parenchymatous cells often arranged concentrically and intermingled with crushed tanniniferous cells. A few sclerotic nests similar to those found in the normal cortex are also present. A careful examination of transverse and longitudinal sections cut through this region has led to the conclusion that the



Text-fig. 3. Transverse section of part of oak stem showing callus tissue formed from living cells of medullary rays.

abnormal tissue has originated in a callus produced by the outgrowth of the living medullary-ray-cells at the surface of the wound: this has in its turn been overgrown by an investing layer produced in the usual way. Apparently the newly-formed layer of normal wood was wounded in much the same manner the following year, and again healed by the development of callus-tissue from the living cells of the medullary rays.

A second slab of oak from the same stem was examined and showed another case of wound healing very similar to the above, but differing from it in that the callus-cushion overarching the abnormal tissue was more distinct.

In this connection it is interesting to notice that Hartig[1] described and figured a case of wound healing in the oak by the formation and fusion of club-shaped swellings from the exposed ends of the medullary rays. The process was, however, not complicated

[1] Hartig. Forstliche Culturpflanzen.

by the additional development of callus-wood from the edges of the wound as in the present instance.

The wound-wood in the vicinity of the rind-galls was also examined in some detail, longitudinal sections as well as transverse being cut where possible. A considerable increase in the amount of wood parenchyma was observed, also the smaller size and more scattered arrangement of the vessels in these regions. The cavities of the vessels were frequently found to be completely blocked with much thickened, lignified tyloses flattened by pressure into polyhedral forms and communicating with one another by means of simple pits. Near several of the wounds these tyloses were packed with starch grains. Thinner-walled tyloses were found to be very abundant in the sap-wood lying to the outside of the embedded peg.

As the tissue of the overarching callus-cushions is much distorted, sections were cut to the right and left of the injuries described above, so as to show the wound-wood in continuity with the normal wood. In several cases the disintegration of a broad ray into a pencil of uniseriate rays was found to occur as the result of the injury, and the gradual compounding of these was noticed. In other cases, however, the rays continued their course undisturbed by the wound-stimulus.

The xylem formed outside the wounded areas after the coalescence of the callus-cushions was also examined. In most cases the wound-wood in these regions showed only non-aggregated small rays. Fig. 2 (Plate II), is a photomicrograph of a transverse section through the wound-wood outside the peg, just where heart- and splint-wood join. Owing to the presence of dark-brown tanniniferous contents in the ray-cells, the compounding process can be seen very distinctly. The *abrupt* formation of broad compound rays was also noticed in the straight grained tissue near several of the injuries, and the same phenomenon was observed in most of the callus-cushions.

During the last two years much has been written regarding the evolution of the different types of medullary rays met with in Dicotyledons and more especially in the Fagales.[1] Eames,[2] from the study of ancestral forms and the development of seedling oaks, has supported the view that the wood of primitive Fagaceæ was entirely devoid of the broad homogeneous "primary rays," which are present together with uniseriate rays in the wood of deciduous

[1] See "Medullary Rays and the Evolution of the herbaceous habit." NEW PHYT., Vol. X, p. 362.

[2] Eames, A. J. "On the Origin of the Broad Ray in *Quercus*." Bot. Gaz., 49: 161-166.

oaks. The broad rays are supposed to have arisen phylogenetically by the fusion of uniseriate rays. Bailey[1] has arrived at the same conclusion from an investigation of the traumatic wood of several species of *Quercus*. In the immediate neighbourhood of a severe wound he found only uniseriate rays produced, though a slight injury occasionally caused the abrupt formation of broad rays. Groom[2] has recently reviewed the position and has given it as his opinion that "it is impossible at present to decide whether in *Quercus* the broad-rayed or the narrow-rayed type was primitive." He has also suggested the possibility of the origin of broad rays in *Quercus* and *Alnus* by a fusion of small rays as being merely of physiological significance.

The European species *Quercus pedunculata* is not included among the species whose traumatic tissues were examined by Bailey, and it is interesting to notice that its behaviour when wounded is not entirely in accordance with the results obtained by the above investigator, since severe wounding does not invariably cause the production of uniseriate or non-aggregated small rays, but occasionally also the abrupt formation of broad rays.

The writer wishes to express her gratitude to Professor Seward for facilities for working at the Botany School, and for advice in the above investigation.

BOTANY SCHOOL,
CAMBRIDGE. *May, 1912.*

[1] Bailey, I. V. "Traumatic Oak Woods." Bot. Gaz., 50: 374-380.

[2] Groom, P. "The Evolution of the Annual Ring and Medullary Rays of *Quercus*." Ann. Bot., Vol. XXV, No. C, October, 1911.

DESCRIPTION OF THE PHOTOGRAPHS ON PLATE II, ILLUSTRATING MISS DUTHIE'S PAPER ON WOUND HEALING IN A SPECIES OF OAK.

FIG. 1. Photograph of slab of wounded oak, shewing the the deal peg and the several wounds described in the text.

FIG. 2. Photograph of transverse section of wound-wood outside embedded peg at the junction of heart and sap-wood, shewing the "compounding" of narrow medullary rays.

FIG. 3. Photograph of tangential section of callus-wood outside jagged end of deal peg, shewing changed shape of rays and twisted course of xylem elements.

FIG. 4. Photograph of transverse section of abnormal callus-tissue formed by the fusion of club-shaped outgrowths from exposed medullary ray cells, shewing regularly arranged groups of very thick-walled fibres in bands alternating with thick-walled wood parenchyma often arranged concentrically: also crushed tanniniferous cells (dark).

A DISEASE OF TOMATOES.

BY F. T. BROOKS, M.A.

(Senior Demonstrator of Botany, Cambridge University),

AND

S. R. PRICE, B.A.

(Frank Smart Student, Cambridge University).

[WITH 13 TEXT-FIGS].

IN October, 1911, some diseased tomatoes grown out of doors in the neighbourhood of Bristol were sent to one of us for examination. These fruits bore large diseased areas somewhat depressed below the surface of the healthy parts. On the diseased portions of the fruits three fungi were found, a species of *Cladosporium*, a species of *Macrosporium*, and a fungus having pycnidial fructifications. These fungi were indiscriminately mixed for the most part, but on some of the diseased areas most recently formed only the fungus bearing pycnidia could be seen. It was thought, therefore, that the fungus with pycnidial fructifications might be the actual cause of the rot, the other fungi having appeared later as saprophytes.

In order to determine which organism was the cause of the disease the three fungi were isolated in the usual way by means of plate cultures. Tomato fruits approaching maturity were inoculated with these fungi in the following manner, one kind of fungus only being inserted in each of the fruits:—in opposite sides of each of three fruits two slits were made with a scalpel, and mycelium taken from a pure culture of each fungus was inserted in them, the fruits being placed on glass plates and covered with glass dishes. Three days later a rot had begun around each of the two slits in which the fungus with pycnidial fructifications had been placed, whereas the tomatoes inoculated with *Macrosporium* and *Cladosporium* respectively remained unaffected. After a fortnight the one tomato was completely rotted, whereas the other two were sound. Hence this preliminary trial made it tolerably clear that the fungus bearing pycnidia was the cause of the rot, the *Macrosporium* and *Cladosporium* being of no significance in this case, although it is well-known that species of both of these genera sometimes cause diseases of tomato fruits. Subsequent experiments with the three fungi confirmed the result of the preliminary trial, *viz*,, that the fungus having a pycnidial type of fructification was the cause of the disease.

At a later date one of a consignment of tomato fruits grown under glass in the neighbourhood of Cambridge was found to be affected with the same fungus, the pycnidia, spores, and characters when grown on artificial media being identical with those of the fungus isolated from tomatoes grown out of doors.

Identification of the Fungus on Tomato Fruits.

As yet few fungi with pycnidial fructifications have been described as causing diseases of tomato fruits. Plowright[1] in a paper on diseases of tomatoes mentions *Phoma destructiva* and *Sphæronema lycopersici* as causing rots of the fruit. The former fungus was associated with a species of *Cladosporium* and a species of *Macrosporium*, both of which Plowright considered to be stages in its life-history; but in the absence of culture and inoculation experiments it is impossible to say whether this was really the case or whether either of these forms was the actual cause of the rot. The characters of *Sphæronema lycopersici* as given by Plowright agree more closely with those of the fungus with which this paper deals and it is possible that they are identical, but Plowright's description of the fungus is too meagre to enable the identity to be established. Massee[2] mentions a pycnidial stage as occurring in the life-history of *Macrosporium solani*, Cooke, which is now considered to be identical with *Macrosporium tomato*, Cooke, the cause of the common black rot disease of tomato fruits, but the characters of the pycnidia do not agree with those of the fungus with which we are now concerned.

Massee has recently described the occurrence on tomato plants in England of the fungus *Diplodina citrullina*, Grossenbacher, or *Ascochyta citrullina*, C. O. Smith, as it is sometimes called, this fungus being the pycnidial stage of *Mycosphærella citrullina*, Grossenbacher. Massee[3] describes this fungus as attacking in an epidemic manner the stems of tomato plants grown under glass. One of us has also had the fungus under observation in Cambridgeshire where it has attacked plots of out-door tomatoes for two seasons in succession. In these cases the lower part of the stem was the region attacked, the cortex being partly destroyed. It occurred to us that the fungus on the tomato fruits might be identical with the *Ascochyta citrullina* mentioned above. The characters of the pycnidia and spores of the fungus on the fruit closely approached those of *Ascochyta citrullina* on the stems of

[1] Plowright, C. B. *The Gardeners' Chronicle*, 1881, p. 620.
[2] Massee, G. *Diseases of Cultivated Plants and Trees*, p. 503.
[3] Massee, G. *Kew Bulletin*, 1909.

tomato plants, and upon sending to Mr. Massee a specimen of the fungus on the fruit, he pronounced it to be "*Ascochyta citrullina*, C. O. Smith, the conidial form of *Mycosphœrella citrullina*, Grossenbacher."

The young pycnidia on the tomato were pale brown in colour, and became darker with age, the spores were hyaline and occasionally uniseptate. The measurements both of the pycnidia and spores were about the same as those given by Massee in his description of *Ascochyta citrullina*. When mounted in water and observed under the microscope, mature pycnidia were seen to liberate their spores in a coil-like manner through the ostiole. The pycnidia obtained from the stems of tomato plants liberated their spores in the same manner.

As material of the fungus was available both from fruit and from stem it was thought desirable to grow the fungus from the two sources on artificial media and to perform inoculation experiments. The fungus obtained from the fruit was placed in the stems, and the fungus from the stem was placed in the fruits. In this manner it was hoped to establish more completely the identity of the fungus from the two sources.

Cultures of the Fungus Isolated from the Fruit.

On account of the method of liberation of the spores it was easy to obtain them in a fairly clean state and establish pure cultures of the fungus. The spores germinated readily both in water and in a dilute solution of sugar.

On tomato extract containing 10 per cent. of gelatine the fungus grew well, forming a dense white mycelium which began to sink into the medium after 8-10 days, at the same time causing liquefaction of the gelatine. The mycelium did not produce spores when grown on this medium.

On tomato-agar, *i.e.*, agar containing tomato extract, the mycelium grew less vigorously but pycnidia developed in considerable numbers. These fructifications were brownish in colour and similar in structure to those obtained on tomato fruits, but were more variable in size. The spores were similar to those produced by pycnidia that developed in the tissues of the plants. In old cultures the spores exuded from the pycnidia and formed blobs of a pinkish colour at their orifices, though the masses of spores sometimes spread over the surface of the pycnidia or the medium in the immediate vicinity. In these cultures there was often a tendency for the pycnidia to be distributed in concentric circles

similar to the manner in which other fungi develop their fructifications on various media, but this tendency was more marked in the case of certain cultures of the fungus originally derived from the stems of tomato plants.

On pure agar the fungus grew much less readily; the mycelium was sparse and only a few pycnidia developed. Fig. 1 represents

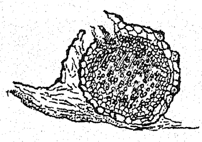


Fig. 1. Fungus isolated from fruit. Section of pycnidium on agar. ×125 diam.

Fig. 2. Fungus isolated from fruit. Fresh spores from pycnidium on agar. ×770 diam.

a microtomed section of one of these pycnidia and Fig. 2 fresh spores from such a pycnidium.

Cultures of the Fungus Isolated from the Stem.

Cultures were obtained in the same manner as in the case of the fungus isolated from the fruit. The spores germinated readily both in water and in a dilute solution of sugar.

On tomato-gelatine a dense white mycelium developed which began to sink into the medium in about 8 days and caused liquefaction of the gelatine. No fructifications were formed in cultures on this medium.

On tomato-agar the mycelium grew less vigorously but numerous pycnidia developed. In appearance and structure these fructifications were identical with those which occurred in cultures of the fungus derived from the fruit. The spores, represented in Fig. 3, were similar and in old cultures were aggregated in the same manner at the orifices of the pycnidia. In these cultures also there was a tendency for the fructifications to develop in concentric circles and in one particular series of plates which were kept in a cool position in a North light during December this distribution was well marked, as is shown in Fig. 11, which is a photograph of one of these cultures. Although many other cultures were subsequently kept under approximately the same conditions, the "fairy ring" mode of distribution of the pycnidia was not again so well marked.

On pure agar the mycelial growth was very thin and only a

small number of pycnidia were formed. Fig. 4 represents a microtomed section of one of these pycnidia.

The above observations make it clear, therefore, that as regards behaviour on culture media the fungi derived from the fruit and stem respectively are identical.

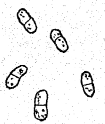


Fig. 3. Fungus isolated from stem. Fresh spores from pycnidium on tomato agar. ×770 diam.

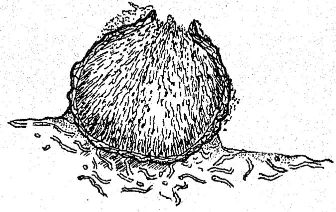


Fig. 4. Fungus isolated from stem. Section of pycnidium on agar. ×770 diam.

Inoculation Experiments with Fungus Derived from the Fruit.

Experiments showed that with green fruits infection would only result if the fungus, either in the form of mycelium from a pure culture on tomato-gelatine, or of spores, was inserted into wounded parts. In such inoculations a rot began in the immediate neighbourhood of the wound a few days after the fungus was

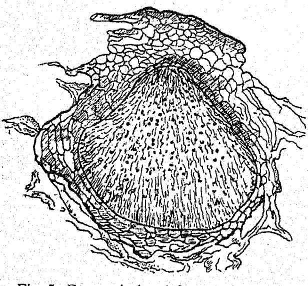


Fig. 5. Fungus isolated from fruit. Section of pycnidium on an inoculated fruit. ×500 diam.

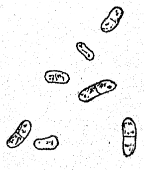


Fig. 6. Fungus isolated from fruit. Fresh spores from pycnidium on an inoculated stem. × 770 diam.

inserted and gradually spread throughout the tissues of the fruit. After 10-14 days numerous pycnidia developed on the surface. Fig. 5 shows a section of one of these pycnidia. The fruits remained

sound in control experiments. With ripe fruits, however, experiment showed that infection sometimes resulted when the mycelium was placed on uninjured parts.

Inoculations of wounded parts of stems of tomato plants were also made with the same mycelium. For this purpose a longitudinal slit was made in the stem about an inch above soil level and some mycelium was inserted, after which the wound was covered with tinfoil. All inoculations were performed as far as possible under

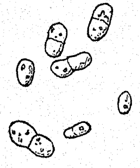


Fig. 7. Fungus isolated from stem. Fresh spores from pycnidium on an inoculated stem. ×770 diam.

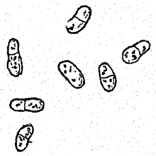


Fig. 8. Fungus isolated from stem. Fresh spores from pycnidium on stem infected in nature. ×770 diam.

sterile conditions. Other plants were kept as controls. The foliage of nearly every plant thus inoculated began to wilt about 7-8 days after the fungus was inserted. Fig. 12 shows one of the wilted plants and one of the control plants side by side. The affected plants subsequently died and in some of them pycnidia of the same character as those previously described, developed in the neighbourhood of the wound. Fig. 6 shows spores obtained from one of these pycnidia. In connection with these inoculations it was noticed

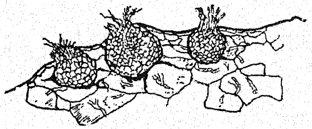


Fig. 9. Fungus isolated from stem. Section of young pycnidia on an inoculated fruit. ×125 diam.

that pycnidia were not formed so abundantly as in inoculation experiments made with the fungus originally derived from tomato stems. To make the story complete the fungus was plated out from these pycnidia and in cultures it proved to be identical with the fungus which had been used for inoculation. Upon examination of the tissues of plants which were successfully infected the

mycelium was found to have extended upwards and downwards both in the vessels and in the cortex. In the few plants which did not become infected after of inoculation, the mycelium had evidently failed to develop.

INOCULATION EXPERIMENTS WITH FUNGUS DERIVED FROM THE STEM.

In almost every case when some of the mycelium grown on tomato-gelatine was inserted in a wound made in the stem of a healthy tomato plant, infection resulted and pycnidia of the same

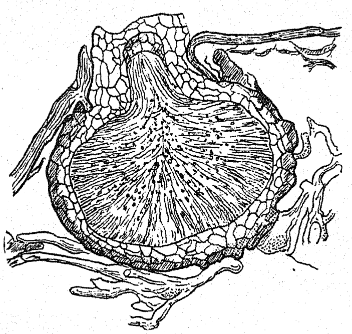


Fig. 10. Fungus isolated from stem. Section of older pycnidium on an inoculated fruit. ×500 diam.

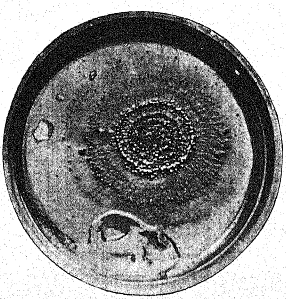


Fig. 11. Fungus isolated from stem. Photograph of culture on tomato agar.

character as those previously described were formed in the tissues. Fig. 13 shows the wilting of a plant inoculated with this mycelium side by side with a control plant. The fungus plated out from these pycnidia agreed in cultural characters with the fungus which had been used for inoculation. Fig. 7 represents fresh spores obtained from these pycnidia. Fig. 8 shows fresh spores obtained from a plant infected in nature.

The same mycelium placed in wounded parts of the fruits caused rotting of the tissues and formation of pycnidia as previously described. The fungus plated out from these pycnidia was identical with that used for inoculation. Figs. 9 and 10 represent sections of these pycnidia in different stages of development.

The results of these inoculation experiments make it clear that the fungus causing a rot of the fruit is identical with that which induces canker on the stem.

Fig. 12. Photograph of plant inoculated with the mycelium of the fungus isolated from the fruit. A control plant is at the side.

Fig. 13. Photograph of plant inoculated with the mycelium of the fungus isolated from the stem. A control plant is at the side.

The Ascus Fructifications of the Fungus.

Grossenbacher[1] has shown in America that *Diplodina citrullina* (C. O. Sm.) Grossenbacher, or *Ascochyta citrullina*, C. O. Smith, as it has also been called, is the pycnidial stage of the Ascomycete,

[1] Grossenbacher, J. G., in N.Y. Agric. Expt. Sta., Geneva, N.Y., Technical Bull. No. 9 (1909).

Mycosphærella citrullina, Grossenbacher. This fungus causes a serious disease of melons in the United States, the pycnidial stage there being followed by the formation of perithecia which, however, do not develop until the tissues are dead or dying. We cannot find any record of the perithecial stage having been found in this country, and in the course of our own work perithecia were not seen, although plants and fruits killed by the fungus were kept in an exposed situation during the winter in order to try to induce their formation.

General Remarks.

As with so many other pathogenic fungi little is yet known of the manner in which infection by this fungus occurs in nature. The facilities which might enable such a matter to be solved have not been available to us. Such problems can be best studied in tomato houses and gardens developed on practical lines, although used primarily for experimental purposes. At present we do not know of any place in England where such work can be pursued in an adequate manner.

In one plot of out-door tomato plants in Cambridgeshire the disease occurred two years in succession, and in view of the apparent absence of a perithecial stage in this country and of the fact that the tomato plant is an annual, it is not clear how the disease is propagated from one year to another. It is possible that the mycelium hibernates in the dead tissues of affected plants, and it may be that portions of diseased plants left on the ground instead of being burnt are the means of reinfection if plants are set out on the same plot the following year. There is no evidence yet that the fungus is propagated in the seed. On out-door plants the disease does not appear to develop until almost fully grown. In the plots referred to above only 3 per cent. of the plants were affected and the distribution of diseased plants was sporadic, so that the disease is not likely to become a serious pest to growers of out-door tomatoes. In the case of tomatoes grown under glass, Massee[1] has already pointed out how severe an epidemic this fungus may cause on account of the conditions of growth being so favourable for its development. In consequence of its virulence under these conditions it is included in the list of pests scheduled by the Board of Agriculture, under the Destructive Insects and Pests Acts.

[1] Massee, G. *Kew Bulletin*, 1909.

NUCLEAR OSMOSIS AND MEIOSIS.

By J. Bretland Farmer.

A THIRD instalment of Professor Lawson's nuclear studies has just appeared in the Transactions of the Royal Society of Edinburgh. In it the author develops further some of the views put forward in his previous memoirs, and makes certain observations in reply to a brief criticism upon them which I contributed a few months ago to this journal (Vol. XI, p. 139, 1912).

I may say at the outset that I observe with great pleasure that Professor Lawson agrees with the results, as regards the essential facts of meiosis, which have been arrived at in my laboratory during the last few years. Differences in detail of course there are, but a near examination lessens their importance and I shall refer to this aspect of the matter later on. It is necessary, however, to enter a little further into his hypothesis of "nuclear osmosis," inasmuch as some of the remarks made in the review referred to above appear to have been misunderstood, and so far as I have been able to discover, none of the criticisms have been met.

I gladly take this opportunity of putting right one point in my previous communication. In discussing Dr. Lawson's statement that no contraction of the chromatic mass occurs during the stage often described as Synapsis, I referred to his own figures, and pointed out that they as a matter of fact did show a very considerable contraction of the chromatic tangle. Unfortunately, however, I included amongst them his Fig. 13, which in the text he had exempted from use in this connection, by saying that it did not represent a median section. In the sentence immediately following it is stated that "All of the other figures [*i.e.*, except 13] were drawn from sections that were cut in a median plane—or nearly so—through the chromatin mass." On turning to the explanation of the figures, however, I find it said of Fig. 13 "The same. The nuclear cavity enlarged still more." And of Fig. 14, "The same, from a section that has not been cut in a median plane throug hthe chromatin mass." There is obviously discrepancy and confusion here, and although I sincerely regret the error which has arisen therefrom, I cannot hold myself to be solely responsible for the mistake.

However, the matter is of no great consequence, for in the Figs. 1—12, about which there is no contention, a contraction of about 25% as compared with Fig. 1 is shown. Any one can easily verify this for himself. It is therefore hardly possible to accept Professor Lawson's statement that "The original paragraph itself is a complete reply to the criticism." I do not think the matter of the diminution in the space occupied by the chromatin is of "secondary importance" as Professor Lawson now suggests. When an author is very confidently indulging in speculation, one may fairly require that facts at any rate should be treated with respect. What may appear to be of "secondary importance" to-day may assume a very different aspect in the light of more complete knowledge, and it is of infinitely greater value, in the long run, to get at the facts than to spin hypotheses, be they never so attractive.

Professor Lawson appears to think I have misrepresented him in my remark as to his use of the term permeable membrane in connection with the alleged osmotic process. He says "The term I have *continually* used throughout the paper is a *permeable plasmatic membrane*" (the italics are his own). In the first place, on turning to the paper itself (Nuclear osmosis, p. 144) I find the following statement:—

> "Everything necessary to promote osmotic diffusion is present, there is a permeable membrane and substances of different chemical composition and presumably of different density on either side of it. It is therefore not difficult to understand the gradual diminution of the karyolymph, as shown in these figures, on the basis of osmotic diffusion. The karyolymph has passed out into the cytoplasm by exosmosis."

Will Professor Lawson, in the face of this quotation, still maintain that I have misrepresented him?

In the second place, even if we waive the question as to the exact nature of the nuclear membrane, and agree to call it a plasmatic one, this is still not *ad rem* in so far as an osmotic process is concerned. It is not with the plasmatic character, but with the osmotic property of the membrane that we have to do. A *permeable* plasmatic membrane would be about as effective in the matter as a permeable or perforated bladder. *Semi-permeability* (or selective permeability) is, of course, one of the essential conditions in the absence of which no osmotic pressure could be either set up or maintained. Is it possible that Professor Lawson himself is not clear as to the difference between osmotic and ordinary diffusion processes? If so his description of chromatin as "an osmotically active substance" at a time when it "is undergoing a change to a more condensed form" (Study in chromosome reduction, p. 604) becomes explicable though it still remains unintelligible.

If, however, Professor Lawson means by exosmosis or "osmotic diffusion" of the karyolymph a mere diffusion of nuclear sap from the nucleus into the cytoplasm, consequent on the abolition of the semi-permeable character of the plasmatic nuclear membrane which was hitherto responsible for the maintenance of nuclear turgor, then any contraction of the latter will depend solely on the surface tension properties of this nuclear membrane. The whole achromatic spindle, supposed to arise through the distortion of the cytoplasmic reticulum which is assumed to be coherent with the membrane, must then be attributed to the effects of surface tension alone. But this aspect of the problem seems to have escaped him altogether, or at any rate it has not been discussed. And in the absence of evidence to the contrary we may be permitted to doubt whether the surface tension of the nuclear membrane under the prevailing conditions would be competent either to produce or to effect such a distribution of strain as would account, in any way whatever, for the origin and peculiar characters of the achromatic spindle.

But Professor Lawson appears to desire to have his cake and eat it—*i.e.*, to postulate a membrane endowed with qualities enabling it to permit of loss through diffusion outwards (exosmosis) while at the same time it is maintaining an osmotic pressure within; for he speaks of the chromatin as an "osmotically active substance" as

effective at a time when, on his own showing, karyolymph is passing out of the nucleus.

I am further charged with having, in my review, passed over "The discovery of the stages showing the persistence of the nuclear membrane throughout the prophase" (*loc. cit.*, p. 617). I am not quite clear wherein the discovery consists. If the alleged closing in of the membrane over the chromosomes and its partition over their several individual surfaces is meant, I would remark that I did refer to this, and with a scepticism which Dr. Lawson's reply has done nothing to allay. If, however, something else is intended I would point out that it has long been known that the nuclear membrane may persist throughout the prophase and even on to the metaphase of mitosis. Such an example is afforded by *Fucus*, which I think would be a difficult case in many respects to reconcile with Professor Lawson's hypothesis; and there are others besides.

It is also alleged that I omitted to mention "Three important phases of mitosis" of which it is suggested that the hypothesis of nuclear osmosis offers "A fair and rational explanation." (i) the origin and formation of the achromatic fibrils, (ii) the attachment of the fibrils to the chromosomes, (iii) the movements associated with the resolution of the multipolar figures into a bipolar arrangement (*loc. cit.*, pp. 616—617). I am at a loss to understand this, because as regards (i) and (ii) I expressly pointed out what appeared to me to be some of the obstacles in the way of accepting the proposed explanation. It seemed to me, and seems so still, that the "explanation" introduces new difficulties without explaining any of the old ones. I may add that the suggested mode of transition from the multipolar to the bipolar position indicated by Dr. Lawson appears to invoke purely gratuitous assumptions as to properties and behaviour of a reticulum under the postulated conditions of strain. I regret that Professor Lawson should apparently have overlooked my remarks on the aforesaid matters, for he is apparently quite unaware of the number of points in which his hypothesis bristles with difficulties. It is of little use to speak of "convincing proofs," "irresistible conclusions" or even of "belief" to those who feel, as I do, that the arguments are fallacious and the conclusions are unsound.

The treatment accorded to the origin and behaviour of the interzonal spindle (*i.e.*, between the two daughter-nuclei during the anaphase) is another example of the way in which awkward points are shelved. The whole development, contour, extension towards the peripheral cell-wall, and especially the appearance and position of the cell-plate, should have all been considered in connection with any comprehensive theory of the mechanics of mitosis. It is not enough to invoke hypothetical relaxation of the fibres, nor to be assured that there "is no doubt" in the author's mind that:—

> "These threads represent the same state of tension expressed in the achromatic figure of the later prophase and metaphase. The lines of tension have merely shifted with the movements of the chromosomes."

A passage of this sort suggests a lack of appreciation of the fundamental distinction between a mere expression of opinion and a scientific reasoned argument.

A series of facts, with which the author has not as yet dealt,

appears to me to be specially difficult to reconcile with the hypothesis that nuclear osmosis constitutes a fact of serious importance in mitosis. It is well known that the whole spindle, in certain cells, may be *intra-nuclear*, and this from the time of its first appearance; and yet the structures themselves so precisely resemble the extra-nuclear spindles in every other respect, that it is impossible to regard them as fundamentally distinct in character. Intra-nuclear spindles have been recognised in a number of animal cells, and the example of *Fucus*, already quoted, is only a little less striking. In the latter plant the spindle is partly extra-nuclear, *i.e.*, cytoplasmic, and partly intra-nuclear, and indeed the nuclear wall persists as a barrel-like body enclosing the spindle and chromosomes even during the metaphase. There is no need to regard the spindle fibres as "pushing into" the nucleus. They appear to originate by differentiation from the nuclear contents, just as the fibrils in the cytoplasm arise, by differentiation, from the cytoplasmic substance. And in both positions they seem to map out lines of force or of strain.

Amongst the numerous points which will have to be worked out in detail in connection with any theory which aspires to explain the mechanics of mitosis will be:—(i) the shape of the spindle, its straight and its convex appearance in profile; (ii) the lack of adherence to the cytoplasmic boundary, so frequently observed, *i.e.*, its differentiation and blind ending in the cytoplasm; (iii) the details of the convergence of multipolar to bipolar arrangements, and the analysis of the causes of these rearrangements; (iv) the definite arrangement of the equatorial plate, and the polarised character of the spindle in the connection therewith; (v) the frequent suppression of the peripherally directed fibres, present in so many cells, during this period of metaphase; (vi) the detailed analysis of the processes leading to the formation of the interzonal spindle—a study of those forms of belated cell-wall formation, *e.g.*, those encountered in some endosperms, might well help to elucidate this; (vii) the intra-nuclear spindle.

Although these suggestions are by no means exhaustive, they may, I think, be taken as representing a fair sample of the problems that have to be faced. It is by no means likely that their entire solution will be achieved in the immediate future, nor indeed until we obtain to a far deeper and more accurate knowledge of the microphysics of the cell, and of the modifications of structure and consistency depending on chemical and physical change, than we possess just now. For the present, then, we must continue to work with hypotheses. But we may reasonably ask that, while embracing the observed facts, these hypotheses should not conflict with the principles of elementary physical science.

We may now leave these matters and turn to the main results of Professor Lawson's most recent communication. Here we reach ground where, happily, a closer agreement is possible. The plant principally selected for the investigation of the meiotic phase was a species of *Smilacina*, and it has evidently turned out to be a most fortunate choice. Some of the stages which have proved troublesome in forms otherwise satisfactory, seem to exhibit a clearness that leaves nothing to be desired. The chief results are, briefly, a follows:—The chromatic substance, as it differentiates from the resting nucleus at the prophase of the first meiotic division is seen

to be double from the first. In this respect Professor Lawson's observations are in precise accord with our own (Farmer and Digby, On the Somatic and Heterotype Mitoses in *Galtonia candicans*, Brit. Ass. Rep., Sheffield, 1910). That is to say, each chromosome arises with a structural arrangement *already in existence* identical with that which finds its expression in the longitudinal fission during the ordinary somatic mitosis. It is this duplex character which has been interpreted by Grégoire and his pupils to represent the lateral approximation of pairs of somatic chromosomes to form the heterotype bivalents, owing to the failure to recognise it at these earlier stages. It appears clear, however, that the explanation advanced by Grégoire cannot be fitted to the case of *Smilacina*, any more than it could to *Galtonia*. Each duplicate filament of *Smilacina*, represents one longitudinally split somatic chromosome, *for they are present in the full pre-meiotic or diploid (2x) number.* There appears to be no room for mistake, inasmuch as they are described and figured as entirely separate from one another, furthermore they are apparently free from lateral or other anastomoses which in *Galtonia* and other plants so often serve to mask or obscure the real course of events. Later on, at a stage corresponding with the "second contraction" of some authors, the split pre-meiotic chromosomes join in pairs, conjugating laterally to form the heterotype bivalent (x) chromosomes. The longitudinal fission in each (pre-meiotic) chromosome persists more or less obviously until the metaphase of the next (homotype) mitosis, when it becomes finally effective and brings about the separation of the daughter chromosomes at this stage.

There is, of course, nothing very new in all this, but it furnishes a welcome and important confirmation of that interpretation placed on the critical stages of meiosis which is becoming more widely adopted at the present time.

It is about ten years ago since several investigators, ourselves among the number, working independently of each other, put forward these views. They were set forth in some detail in a paper published in 1905 (Farmer and Moore) to which Professor Lawson makes frequent reference. With the increase of knowledge, amplification and corrections in detail have naturally been made, but the main results then reached have been, in essentials, confirmed by further research on the part of my co-workers and myself, as well as by others. Different material varies greatly, both as regards the clearness with the process can be followed, and the certainty with which the evidence can be sifted, and it is to this circumstance that the divergence of views which still exists is to be largely attributed. In this connection the investigations on hybrid and mutating plants have proved of especial value. Thus Gates has observed important stages in his studies on *Œnothera* (subsequently confirmed by other students of the cytology of this genus) which appear to be irreconcilable with the very different explanation first advanced by Grégoire and his pupils.

It is unnecessary for me to enter at greater length into the controversy which has been going on for a number of years concerning the time at which meiotic pairing of the chromosomes to form the bivalents occurs. Nor is it necessary to discuss the radically different interpretations which have been placed on the

parallel threads that can be observed during the early stages of prophase as I have already given a brief epitome of them in a recent note on "Telosynapsis and Parasynapsis" in the current volume of the Annals of Botany.

Professor Lawson, in quoting the work which has issued from this laboratory, curiously enough rather exaggerates points of difference between us, but it seems a pity that in doing so he should have imputed to us opinions which are the very reverse of those which we have advanced. I do not propose to enter at full length into this matter, for controversy on matters of history where the evidence is readily accessible is useful only in so far as it serves to prevent error from becoming stereotyped, as it is apt to do if allowed to go entirely unchallenged.

Professor Lawson states on p. 605 :—

> "But this diminution [in the chromatin volume], which is a very slight one, I do not interpret in any sense as a 'synaptic contraction' as generally understood by many writers (Farmer, 1905; Grégoire, 1910; Overton, 1909; Digby, 1910, and others, and others), nor do I believe it to be a feature peculiar to meiosis."

Now this is thoroughly misleading, for while Grégoire and his followers have regarded the conjugation of the somatic chromosomes as the essential features of this stage, my co-workers and I have simply regarded it as a puzzling feature which we were bound to accept, though we could not explain it. But we have held that what Grégoire believes to indicate lateral approximation of somatic (or premeiotic) chromosomes in reality represents the *longitudinal fission of the spireme*, precisely as Professor Lawson appears to do. And confirmatory evidence of this has been advanced both by Dr. Fraser and by ourselves in several papers published during the last two years.

There are other passages in which Professor Lawson betrays a singular lack of critical historical feeling; I will only quote one example :—

> "It should be remembered that the interpretations of Farmer (1905) .... are based on the assumption that the chromatin consists 'of one continuous spireme, which segments transversely so as to form definitive chromosomes.'"

Such a statement is not in accordance with fact, it does not fairly describe our position in 1905, and still less does it represent the views we have advanced in more recent papers. It is quite true that we frequently spoke of a continuous thread, for in 1905 the opinion was almost universally held that the spireme did consist of an unbroken thread, which only later segmented and formed the chromosomes. But we ourselves ventured to throw doubt on the view, and described examples in which there was definite proof either that a continuous spireme was never formed (*Blatta*), or that at any rate that it was not present in the early stages (*Tradescantia*), "It is quite certain that during these early stages of prophase there is no continuous spireme present. The ends of the stainable threads can be clearly recognised." (Farmer and Shove, Q.J.M.S., 1905, p. 653). Furthermore, in discussing the question

as to whether or not there is a continuous spireme in *Lilium*, though it was believed that such was formed later on (and as I now think erroneously), it is remarked, "perhaps the matter is not of very great importance." .... (Farmer and Moore, 1905, *loc. cit.*, p. 508).

The belief in a continuous spireme, so prevalent at that time, was, as a matter of fact, one of the serious theoretical difficulties we had to encounter in arguing for the persistence of chromosomes from one cell generation to another, and we devoted considerable space to the attempt to show that the commonly entertained belief was not really well founded (*loc. cit.*, pp. 543-5). And with the advance of knowledge we, with others, have accepted the possibly morphological, as well as the physiological, individuality of the chromosomes in the spireme, as well as during other phases in the life history of the nucleus.

The principal credit for the recognition of this independence of the chromosomes during the spireme stage of prophase belongs unquestionably to Grégoire and his pupils. Nor does any difference of interpretation of the events of "synapsis" seriously touch this claim, though it does somewhat affect the supposed evidence on which the generalisation itself was based.

Professor Lawson draws attention to the well nourished condition of the spore mother-cells, and he appears to see in this accumulation of available nutrative material an explanation of the rapid succession of the two meiotic divisions. Discussion of the points raised by this or kindred suggestions would be out of place at the present time, inasmuch as a further paper is promised wherein the author expects to deal more fully with this important question.

IMPERIAL COLLEGE OF SCIENCE
AND TECHNOLOGY, *December 2nd, 1912.*

RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

BY F. CAVERS.

I—INTRODUCTION.

TWENTY years ago Klebs (67)[1] published the first comprehensive work on the Flagellata in which these organisms—usually treated by zoological writers as a division of the Protozoa—were studied in detail from the botanical as well as the zoological point of view. Klebs pointed out that the Flagellata are a heterogenous assemblage in which, more than in any other Protista, the former distinctions hitherto drawn between the animal and vegetable kingdoms entirely vanish; that the Flagellata may be regarded as a central group from which the various classes of Protozoa have arisen; and that this group also embraces a number of specialised lines of descent—including several distinct lines

[1] References to Literature will be given in a Bibliography at the end of the concluding portion of this article.

leading to the lower Algæ. The results of recent work, some of which it is proposed to summarise and discuss here, have in the main confirmed the views expressed by Klebs in his diagrammatic scheme of the phylogenetic relationships between Flagellata and Algæ—with certain modifications arising from the discovery of new forms and the reinvestigation of forms whose structure and development had been imperfectly known—and have lead to great advances in our knowledge of the phylogeny of the Algæ, and to striking changes in the classification of the Green Algæ in particular.

It is now generally recognised that a division of the Flagellata into forms referable to the vegetable kingdom (forms bearing chlorophyll, having a cell-wall of cellulose, and having no mouth or other means for ingesting solid food) and forms referable to the animal kingdom (forms without chlorophyll, without a cell-wall or with a wall not consisting of cellulose, and having a mouth or other means for solid ingestion) would be absolutely unnatural and could only be made by ignoring genetic relationships which are perfectly obvious. Moreover, such a division would leave out of account a large number of organisms which could not logically be placed in either division. A better criterion would seem to be afforded by the consideration that in the lowest organisms regarded as animals, somatic growth and reproduction by fission are marked by active mobility, the flagellate cells growing and dividing in this condition; whereas in the lowest organisms regarded as plants, somatic growth and division are marked by stability, and the flagellate cells do not grow and divide but may conjugate and give rise to a sedentary zygote. We shall see, however, that even this criterion—which has led to the inclusion by zoological writers of the greater part or even the whole of the Flagellata in the animal kingdom as a class of the Protozoa—is vitiated by the occurrence of transitional forms through which certain Flagellate groups shade off almost imperceptibly into definitely Algal organisms.

Assuming that the lower Algæ have arisen from a Flagellate ancestry, the work of the majority of recent writers on the phylogeny of the Algæ has been directed towards the tracing of the lines of descent leading from certain Flagellate groups to the lower Algæ, and to the formulation of a system of classification which shall reflect the phylogenetic relationships thus disclosed. Of the four main groups into which the Algæ have usually been divided, the Blue-green Algæ are probably related in some way to the Bacteria, but the origin and affinities of both divisions of "Schizophyta" are quite uncertain, though they are possibly of Flagellate origin; the Green Algæ may be traced, through transitional forms, to at least two distinct sources among the green Flagellata; the Brown Algæ have similarly been shown, especially by quite recent work, to have arisen from certain Flagellata with brown chromatophores; while as regards the Red Algæ there appears at present to be no better-founded view than that suggested by Klebs—that they may have arisen from Brown Algæ.

In recent speculations concerning the evolution of plants it has generally been assumed that the earliest vegetable organisms possessed chlorophyll and were autotrophic (photosynthetic) forms, their immediate ancestors being autotrophic Flagellates;

that the Green, the Brown, perhaps also the Red, and more doubtfully the Blue-green Algæ arose respectively from similarly coloured Flagellata; and that the various groups of Fungi have arisen independently from different Algal forms—though some fungal series may have come directly from Flagellata. However, Vuillemin (144) has pointed out that in our ignorance concerning the conditions under which the earliest forms of life appeared, we are hardly justified in assuming that photosynthetic organisms necessarily preceded heterotrophic organisms in time, and that from this point of view the nitrogen-fixing Bacteria have as good a claim as chlorophyll-bearing organisms to be regarded as the nearest living representatives of the earliest forms of life. We cannot, however, construct a series of existing forms connecting the Bacteria with the main autotrophic Algal phyla, though it has been suggested (Doflein, 40; Zuelzer, 158) that the Bacteria may have given rise, through the Spirochætes, to the Flagellata.

Starting from simple coloured autotrophic organisms, Brunnthaler (6) argues that the Red Algæ are the most ancient group of plants, on the grounds that (i) the earliest plants were in all probability free-swimming Flagellate forms, and no such forms occur among the present-day Red Algæ; (ii) the red pigment of the Rhodophyceæ is an adaptation to life in the deeper waters of the sea and in the dim light of the primitive world with its dense cloud canopy, since this pigment absorbs the rays in which that light would be rich; (iii) the present-day Red Algæ show hardly any primitive types, and motile free-swimming reproductive cells are absent from the group. The Brown Algæ would come next; that this is a younger group is indicated by the great diversity in structure of the reproductive organs, the constant presence of flagellate reproductive cells, and the adaptation of the brown pigment to the absorption of light more closely approaching in quality that of the bright sunlight reaching the surface of the present world, but still with an atmosphere richer in water vapour than that of to-day. Meanwhile, the primitive Red Algæ had become adapted to the dim ancient light, and therefore restricted to the deeper sea, leaving the upper waters as an open field for the evolution of the new brown seaweed population. The Green Algæ, finally, are the youngest group to appear in the succession outlined by Brunnthaler, their green colour being an adaptation to the fuller light (richer in the less refrangible rays of the spectrum) of modern times; the early forms were marine, but after possessing the upper waters of the sea and invading estuaries they became adapted also for life inland in fresh water. According to Brunnthaler, there is no direct relationship between the present-day Algæ and Flagellata, though the earlier Flagellates may have given rise to the Red Algæ; the living Flagellata he regards as the termination of an ancient series of organisms which have evolved independently of the Algæ.

II—General Characters of the Flagellata.

Without dealing further with such questions as these, it may be noted in passing that there is a good deal to be said against the assumption, which has frequently been made, that the Flagellata represent the most primitive of known organisms; this claim may

perhaps quite as reasonably be put forward for bacterial forms or for the simpler amœboid types of Protozoa. For instance, there are grounds for regarding a flagellum as a specialised type of pseudopodium, since between the blunt pseudopodium of an *Amœba* and the vibratile flagellum of a typical Flagellate, there are various intermediate forms of protoplasmic outgrowth concerned in locomotion or ingestion of food or other functions. In any case, however, the Flagellata appear to include forms leading by a series of transitional types to the lower Green and Brown Algæ, and these are our chief concern here.

The characters given by Klebs as distinguishing the Flagellata from the motile unicellular Green Algæ—the Chlamydomonads, which are still included by zoological writers in the Flagellata under the name "Phytoflagellata"—may be enumerated as follows. Body unicellular or a colony of cells, cell uninucleate with a thick or thin external layer of protoplasm—the *periplast*—in which *amœboid changes of form* may take place. Outside this a non-living investment of the cell is frequently present, of varied form and often not closely adherent to the body. Specialised anterior end of clear protoplasm bearing one or more flagella. Organism always remaining capable of movement. Nutrition either *holozoic* (solid food being taken by pseudopodia, through a specialised mouth, or otherwise), *saprophytic or holophytic.* In the last case the chromatophores are green or yellow-brown, and may take the form of bands, plates or discs. *True pyrenoids entirely absent.* Paramylum, leucosin, or a fatty oil the visible anabolites (products of assimilation). *Starch entirely absent. Reproduction by simple longitudinal fission*, usually beginning at the anterior end of the body. Individual always capable of forming resting cysts. *Gamogenesis apparently entirely absent.*

It may be noted that recent work has made it extremely difficult to frame a definition of the Flagellata which shall separate this group sharply from the Protozoa on one hand and the lower Algæ on the other. Exceptions have to be admitted in connexion with almost every character hitherto given in definitions of the group. The body usually has a definite anterior end from which one or more flagella arise, but in *Multicilia* the numerous flagella spring from various points of the spherical body; the flagella are usually motile and unbranched organs, but in certain Chrysomonads they are non-motile and even branched, corresponding with the pseudopodia of various Protozoa; the visible product of anabolism is usually either oil or leucosin or paramylum, but starch is formed in certain Chrysomonadineæ (e.g., *Cryptomonas*) and in the Polyblepharidaceæ (if these be regarded as Flagellates rather than Chlamydomonadine Algæ); the great majority are uninucleate, but the Trypanosomes have two nuclei, while *Multicilia lacustris* is described as having a large number; as a rule, division is longitudinal and occurs in the motile phase, but it is sometimes transverse (e.g., *Oxyrrhis, Stylochrysalis*) and it may occur exclusively in a resting state; sexual reproduction is usually absent, but a sexual process has been shown to occur in various genera belonging to different groups of Flagellata (39, 50, 118, 121).

In Senn's account (135), which was published in 1900, the Flagellata fall into seven divisions. Three of these comprise only colour-

less heterotrophic forms (with holozoic, saprophytic, or parasitic nutrition), while the members of the remaining four divisions are normally provided with pigments which make holophytic nutrition possible, though many of these are also capable of heterotrophic nutrition and may therefore be described as "mixotrophic." In the lowest of the colourless groups in Senn's arrangement, the Pantostomatineæ, any portion of the body can ingest solid food by means of pseudopodia, while in all the remaining forms capable of holozoic nutrition such ingestion occurs only at certain definite points; the Pantostomatinean genus *Multicilia* has a spherical protoplast with numerous radially arranged flagella, but in all other Flagellata the body shows radial or bilateral symmetry, or may be asymmetrical, and the number of flagella is more limited. According to Senn, the Pantostomatineæ have given rise to the lower Protozoa (Sarcodina); to the small Flagellate group Distomatineæ with irregular bilateral symmetry and paired groups of flagella—this group forming a blindly-ending line; and to the very large group Protomastigineæ which comprises about half of the known genera of Flagellata and shows great variety in form and structure. The Protomastigineæ may be regarded as the common source of the Infusoria, Mycetozoa, Sporozoa, and perhaps also the Bacteria, on one hand, and of the four groups of pigment-bearing or "Algal" Flagellata on the other. Of these latter, the Chrysomonadineæ and the Cryptomonadineæ are, according to Senn, closely related but of independent origin; the Chrysomonadineæ have brown chromatophores, produce oil and leucosin, and show affinities with the Brown Algæ and the Diatoms, while the Cryptomonadineæ produce starch, are variously coloured or in some cases colourless, and may have given rise to the Peridiniales and the Green Algæ. The two remaining groups, Chloromonadineæ and Euglenineæ, differ from the other groups in having numerous green chromatophores; there is a more definite periplast or firm outer protoplasmic layer; the contractile vacuoles are so situated and co-ordinated as to form a pulsating system opening at a definite point on the exterior; the product of assimilation is oil (Chloromonadineæ) or paramylum (Euglenineæ). In the Chloromonadineæ, which Senn derives from *Monas*- and *Bodo*-like form among the Protomastigineæ, the contractile vacuoles are aggregated at the anterior end of the cell and open to the exterior by a pore. Senn regards the Chloromonadineæ as being too highly organised to serve as the starting-point for an Algal group as suggested by Luther and others (see below); but they have by further elaboration of the cell given rise to the Euglenineæ, a blindly-ending line representing the highest type of organisation found in the Flagellata and decidedly showing no Algal affinities, whatever may be said of the Chloromonadineæ. The Euglenineæ have, as compared with the Chloromonads, a more definite, often striated, and highly resistent periplast, and a gullet-like canal leading to a deep-seated vacuole into which a system of small and actively contractile vacuoles is drained.

Apart from Senn's compilation, the more comprehensive accounts of the Flagellata are contained in zoological works (18, 19, 37, 40, 93, 138, 150), and much of the recent literature on the "Algal" form is published in zoological journals. The Peridiniales will be dealt with in this review, since this group includes decidedly Flagellate forms, and reference will also be made to certain other

groups (*e.g.*, Crystoflagellata, Silicoflagellata, Coccolithophoridæ) not classed by Senn among the Flagellata, though they occupy this position in zoological systems of classification. On the hand, the Trypanosomes and the majority of the other specialised heterotrophic Flagellata need not be considered in a discussion of the origin of Algæ from Flagellata.

In the following pages, it is proposed, taking as a starting-point the treatment of Algal groups in Engler and Prantl's Pflanzenfamilien and that of the Flagellata in the same work and in the more comprehensive zoological treatises, to review briefly the advances that have recently been made in our knowledge of certain lines of descent leading from Flagellata through transitional forms to the simpler Algæ. Restricting our speculations to such series as appear to include what may be fairly considered as transitional forms, we can recognise three main lines, leading (i) from the simpler Chloromonads to the Heterokontæ or Yellow-green Algæ; (ii) from the Polyblepharids to the Chlamydomonads and thence to the Isokontæ and other Green Algæ? and (iii) from the Chrysomonads and Cryptomonads to the Brown Algæ, the Peridiniales, and probably certain other groups.

III—Chloromonads and Heterokontæ ("Confervales," "Yellow-Green Algæ").

Until recently the Green Algæ have usually been divided into Conjugatæ, Protococcoideæ, Confervoideæ, and Siphoneæ—the division made, for instance, by Wille in Engler and Prantl's *Pflanzenfamilien* in 1890, and adhered to, with slight modifications, in that writer's recent supplement on the Chlorophyceæ in the same work (150). The Conjugatæ form a natural group, marked by the absence of ciliated reproductive cells—whence the name Akontæ given to the group in the modern system of Green Algæ based in part upon the ciliation of the asexual reproductive cells or zoogonidia—and by the siphonogamic sexual process of conjugation by means of a tube formed by the fusion of processes from the two gametangia. The limits and arrangement of the three remaining classes have, however, been considerably modified, owing chiefly to considerations advanced in publications by Chodat, Bohlin, Luther, and Blackman.

In all Green Algæ excepting the Conjugatæ (Akontæ), the zoogonidia and zoogametes are typically pear-shaped cells bearing at the anterior end a number of flagella. In most cases there are two (occasionally four) flagella of equal length inserted at the same point (Isokontæ); in the small order Œdogoniales the motile cells have a circlet of numerous flagella (Stephanokontæ); while in the Confervales there are two flagella of unequal length (Heterokontæ)—in some forms the shorter flagellum may, apparently, be absent. It may be added that in the attempts that have been made to connect Algal series with corresponding Flagellate series, the number and insertion of the flagella are not the sole criteria used, various other characters being taken into account. In certain groups of Flagellata, *e.g.*, the Euglenineæ, the flagella show considerable differences in genera which are obviously related closely to each other as judged by other cytological characters. When due attention is paid to the *tout ensemble* of characters, however, there can be little doubt that the flagellum characters (number, insertion,

relative length where two or more are present) may afford a valuable clue to affinities.

In 1899, Luther (90) described a new genus, *Chlorosaccus* (Fig.

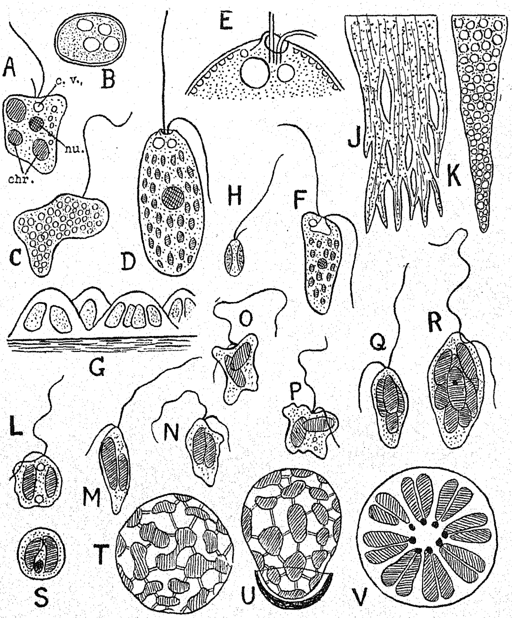


Fig. 1. CHLOROMONADINEÆ (Flagellate and Transitional Heterokontæ). A to C, *Chloramœba heteromorpha* Bohl.: A, a normal green individual, with nucleus, contractile vacuole, three chromatophores, and oil-drops; B, resting cyst; C, amœboid colourless individual. D, E, *Vacuolaria virescens* Cienk.: E shows the anterior end more highly magnified, with two vacuoles and insertion of flagella in the gullet-like pit. F, *Vacuolaria flagellata* Senn. G, H, *Chlorosaccus fluidus* Luther; G, portion of a colony; H, motile cell. J to V, *Leuvenia natans* Gardner; J, a portion of the floating colony; K, the same more highly magnified; L, a motile cell soon after being set free; M, N, O, P, later stages showing amœboid habit of the zoogonidia; Q and R, zoogonidia with four and eight chromatophores respectively; S, resting zoogonidium with the flagella withdrawn and with a cell-wall developed; a free floating colony showing the rapidly dividing chromatophores held together by protoplasmic threads; U, an earlier stage in development of colony, showing the ruptured cyst-wall at base; V, section through a young colony showing the nuclei and the chromatophores in pairs.

A—C from Bohlin; D, E, from Senn; F, from Stokes; G, H, from Luther; J—V, from Gardner.

1, G, H), which is of great importance as forming a connecting link between the Chloromonad genus *Chloramœba* (Fig. 1, A—C) on one hand and the Algal group "Confervales" on the other. This group had been previously founded as a distinct series of Green Algæ as the result of the work of Borzi (14, 15) and of Bohlin (10) on various genera which had formerly been included in the old groups of Protococcoideæ, Confervoideæ, and Siphoneæ. These genera differ from other Green Algæ in several characters besides the possession by the motile cells of two unequal flagella—namely, the presence of a large proportion of xanthophyll or carotin in their chromatophores (hence the name "Yellow-green Algæ" has been given to the group) which are typically numerous and discoid; the production of oil instead of starch as the visible anabolite; and the curious structure of the cell-wall in some genera, *e.g.*, the unicellular *Ophiocytium* in which the upper part of the wall becomes detached like a lid, and the filamentous *Tribonema* in which each cell is bounded by the halves of two H-shaped pieces and the whole filament readily breaks up into fragments of this shape. Luther and Bohlin concluded that these forms had arisen independently of the remaining Green Algæ, from the simpler types of the Flagellate group Chloromonadineæ, e.g., *Chloramœba*, through a transitional form like *Chlorosaccus*. On the other hand, *Chloramœba* leads through forms like *Vacuolaria* (Fig. 1, D—F) to the more specialised Chloromonadineæ and doubtless to the Eugleninеæ, which need not be further considered here.

The genus *Leuvenia* (Fig. I, J to V), recently described by Gardner (48), appears to be related to *Chlorosaccus* and to form an interesting additional link in the chain connecting *Chloramœba* with the "Convervales." The motile cells are at first pear-shaped, with two unequal flagella and two ovoid curved green chromatophores (sometimes becoming four or eight by division); later the cell becomes amœboid. Growth occurs in a resting condition—the motile cells come to rest, float to the surface of the water, become spherical, withdraw their flagella, and grow rapidly in size; then the nucleus divides into as many as twenty, the chromatophores divide by constriction, and finally the whole interior divides up into zoogonidia, each appropriating two chromatophores and a nucleus. Under certain conditions the resting cells secrete a gelatinous substance causing them to adhere together in stringy floating masses, in which they become spherical; and in this palmella stage division into zoogonidia occurs as in the ordinary growth stage.

Pascher (112) has recently described a new genus of Heterokontæ (*Pseudotetraëdron*, which superficially resembles the Protococcaceous genus *Tetraëdron* but shows characteristic Heterokontan features—numerous discoid yellow-green chromatophores, production of oil instead of starch, cell-wall consisting of two portions fitting upon each other like a box and its lid.

Adopting the terminology suggested by Pascher (113), the following arrangement of the Heterokontæ may be proposed. It will be noted that the group is here divided into a series of orders which show a striking parallelism with the corresponding divisions of the Isokontæ. The genera of the Isokontan groups are omitted.

HETEROKONTÆ.	ISOKONTÆ.
HETEROCHLORIDALES. *Chloramœba.* *Stipitococcus.*	VOLVOCALES.
HETEROCAPSALES. Heterocapsaceæ. *Leuvenia* (?) *Chlorosaccus.* *Racovitziella.* Botryococcaceæ. *Botryococcus.* *Askenasyella.* (?) *Oodesmus.* Mischococcaceæ. *Mischococcus.*	TETRASPORALES.
HETEROCOCCALES. Chlorobotrydaceæ. Chlorobotrydeæ. *Chlorobotrys.* *Botrydiopsis.* *Polychloris.* *Centratractus.* *Pseudotetraëdron.* *Meringosphæra* (?) *Bohlinia* (?) Chlorothecieæ. *Chlorothecium.* *Characiopsis.* *Peroniella.* Sciadiaceæ. *Ophiocytium.*	PROTOCOCCALES.
HETEROTRICHALES. Tribonemaceæ. *Tribonema.* *Bumilleria.* *Monocilia.*	ULOTRICHALES.
HETEROSIPHONALES. Botrydiaceæ. *Botrydium.* Vaucheriaceæ. *Vaucheria.* (?) *Dichotomosiphon.*	SIPHONALES.

(To be continued.)

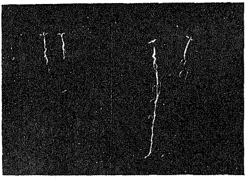


Fig. 1c. Fig. 1d.

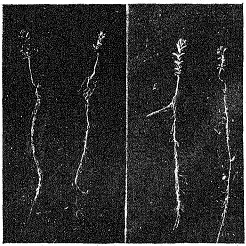


Fig. 1b. Fig. 1a.

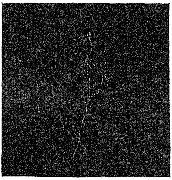


Fig. 5.

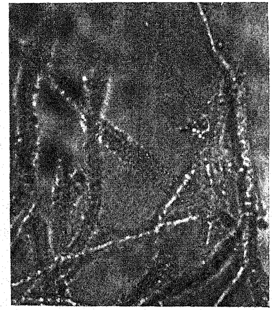
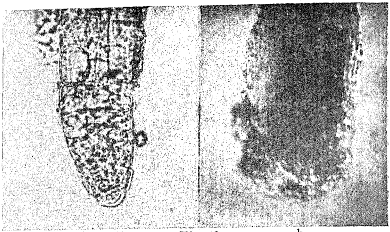


Fig. 6.



a. Fig. 2. b.

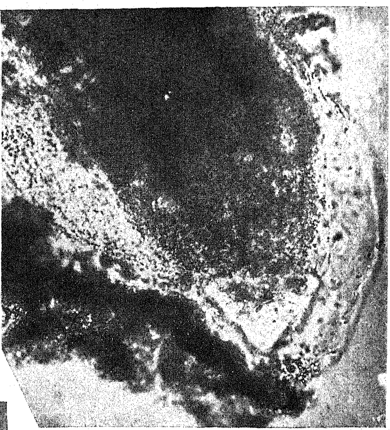
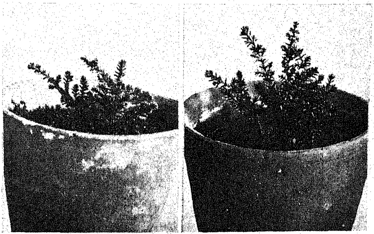


Fig. 3.



a. Fig. 4. b.

THE

NEW PHYTOLOGIST.

VOL. XII, No. 2. FEBRUARY, 1913.

[PUBLISHED FEB. 28TH, 1913].

THE VEGETATION OF JAPAN.

BY H. TAKEDA, D.I.C.

(Demonstrator in Botany, Royal College of Science, London).

I.—INTRODUCTION.

MANY valuable and interesting papers dealing with certain constituents of the flora of Japan have been published by not a few botanists, both Japanese and foreign. Yet there has been lacking, so far as I am aware, a general account of the flora or vegetation of Japan, except perhaps in the form of a catalogue or enumeration of plants growing in that Empire. It has been suggested therefore that a brief description of the vegetation of Japan would be interesting to the readers of this journal. The present paper has been re-written from lectures addressed in 1912 to the Natural History Society of the Imperial College Union and to the Botanical Society of London, and it is proposed therein to give a general idea of the vegetation of Japan.

II.—GEOGRAPHICAL FEATURES AND CLIMATE OF JAPAN.

The position occupied by Japan is somewhat similar to that of Britain, with this difference, that while the British Isles lie on the west of the European continent, the Islands of Japan are to the east of the mainland of Asia. Taking them in the order from north to south, the group of islands comprised in the present Empire of Japan consists of the Kurile Islands, the southern half of Saghalien, Yezo, the main island known to the Japanese as Hontô and occasionally called by Europeans Nippon, Shikoku, Kyûshû, the Loochoos, Formosa, and the Pescadores. These islands stretch diagonally from the 52nd down to the 21st degree of north latitude, and are situated between the 120th and 156th degrees of longitude east of Greenwich. The above described area of the Empire was

increased in August, 1910 by the annexation of Corea, so that it has now much the same area[1] as that of Austria-Hungary, and the population[2] is nearly equal to that of Germany. A warm current called "Kuroshio", similar to the Gulf stream of northern Europe, originating between Luzon and Formosa, flowing past the eastern side of the latter and along the southern Loochoos, reaches the southern extremity of Kyûshû, where it divides into two branches. Whilst the main stream bends northward and flows along the south-east coast of Kyûshû, Shikoku, and Hontô, the smaller branch washes the west of Kyûshû and the Gotô group and runs up to the Sea of Japan through Tsushima or Krusenstern Strait. This so-called Tsushima Stream flows over the eastern half of the Sea of Japan from the south-west to the north-east and passes partly through Tsugaru Strait, but mainly through Lapérouse Strait, and soon dimishes when it reaches the southern part of the Sea of Okhotsk. The main division of the "Kuroshio" bends out into the Pacific Ocean about the 39th degree of latitude and takes a course towards the south of the Aleutian Islands and the coast of North America.

The cold currents in the northern Pacific Ocean, which affect the climate of Japan, originate partly in the Sea of Okhotsk and partly in the Behring Sea. The Kurile Stream, the most important of these, starts in the Penshina and Gishiga Bays and flows southwards along Kamtschatka, and then taking up a weaker current from the eastern side of this large Siberian peninsula, turns towards the Kuriles and washes the whole length of the chain of islands. The current then runs chiefly along the east-coast of Yezo, down to the 39th degree of latitude,[3] where the above-mentioned main stream of the warm current bends away into the Pacific Ocean. The water of this current is very cold and even in the summer its temperature does not rise above 5°C.

These warm and cold currents exercise great influence over the distribution of seaweeds. This is clearly seen on the east coast of Japan, the 39th degree of latitude being the separating point of two different algal floras. On the west coast, however, the course of the currents is more complicated, so that the elements of different floras appear somewhat intermixed, as will be seen from the following examples.

The strand-flora is similarly affected, the northern elements

[1] 256,033 square miles. [2] 63,037,518. (Estimated in August, 1912).
[3] Occasionally it comes down as far south as the 38th degree.

being distributed in the localities touched by the cold currents. To give some examples: *Mertensia maritima* is to be seen in the Okhotsk region, on the coast of Manchuria down to North Corea, while in the main island of Japan and especially on its east coast it is found northward from the 38th degree of latitude. Strictly speaking this plant, as it grows in the Far East differs, from the typical form of Europe and America, in having a stouter stem, and larger and more showy flowers, and it is recognised as a sub-species under the name of *asiatica*.[1] This sub-species is also found in various places on the Behring Sea. *Glaux maritima*, another arctic plant, which we meet with in various places in the British Isles, is distributed in Japan mainly from Yezo northward. But we also find this pretty seashore plant at a spot on the western coast of Hontô, whither the plant has probably been carried by the cold currents. *Plantago camtschatica* is another plant which is to be found in the localities visited by the cold currents.

The warm current has a similar influence on the distribution of plants; it is the important current by which our ancestors reached Japan in remote antiquity.[2] As this current comes into direct contact with the southern parts of Kyûshû, Shikoku, and Kii, various sub-tropical plants are found in these places. To give a few examples: *Rhizophora mucronata* is found at Kagoshima (32° N.L.); *Senecio scandens* in Tosa (Shikoku) and Kii; *Pteris Wallichiana* in Kii; *Asplenium Nidus* in Kii and the Gotô group; *Ipomæa biloba* (=*I. pescapræ*), in Echigo. *Statice japonica* which is mainly distributed in south-western Japan, is also to be found on the east coast as far north as the 38th degree of latitude.

Leaving the coast, let us now proceed inland and see what the country is like. The islands comprising Japan are all mountainous; there is no place from which we cannot see a prominent hill. Not a few of the smaller islands simply consist of one or more volcanoes. The great majority of the high mountains are densely clad with luxuriant vegetation from the foot right up to the summit—often so densely indeed, as to render the thick mountain-forests almost impenetrable. The mountains are generally lofty and exhibit the finest scenery of the country. The grandest mountain-chains are to be seen in Central Japan where they form the back-bone of Hontô, rising in places to an elevation of 10,000 feet. The higher peaks are made up partly of palæozoic, partly of plutonic, and partly

1 Cf. *Journ. Bot.*, 1911, p. 222.

2 Said to have been some 3,000 years ago.

of volcanic rocks. The youngest of the volcanic rocks, the andesite, broke not only through the various sedimentary rocks, but also through the granite, porphyry, and liparite. Although their altitude is so considerable, the mountains of Japan contain no glaciers, but slight traces belonging to an earlier period were discovered in 1902. There is, however, a great deal of névé present on some of the mountains. Mountaineering amongst the high peaks is very instructive, but the ascent is sometimes impeded by thick forest, so that it is necessary to follow a torrent, crossing it again and again until a waterfall intervenes, and then the bank has to be climbed. Sometimes the ascent is made by climbing a field of perpetual snow filling up a gully. Little mountaineering was done, except on certain peaks, until 1905, when the Alpine Club of Japan was organised. Since then very many men have spent their holidays amongst the mountains, climbing peaks where no educated person had been before, or following along huge mountain-chains, to find some new route, or discover new plants.

As the mountainous character of the country would suggest, Japan is naturally very rich in water. A dense network of rivers, torrents and lakes is to be seen nearly everywhere. With a few exceptions, the rivers are short and their gradient steep, causing frequent floods. In the late spring, when the snow which has gathered in the mountains during the winter, begins to melt, or when in the summer the continuous rain carried by the S.W. monsoon frequently falls in torrents, the water flows down in every mountain-furrow, and converts the small cheerful mountain-rivulet into an enormous stream. With the clashing of the muddy water, mixes the thundering sound of pieces of rock rolling over the bottom, carried down by the waves together with the lightly-built bridges and planks. Further down even the solid banks, carefully constructed on both sides of the wide stream, are not always able to withstand the power of the great mass of water or to check its work of devastation.

The numerous waters add a special charm to the magnificent woodland scenery of the mountains. The small stream, rich in trout, carries its clear waters in many directions, sometimes passing huge rocks adorned with pretty shrubs and ferns, sometimes spreading over a boulder, then narrowing into a rocky gorge shaded by bushes and foliage, here hurriedly setting over rocks and covered with white foam, there slowly winding round a projecting rock which appears to arrest its course. Where the water has hollowed

out the bed, the purest blue green of the clear water may be enjoyed. It is generally considered in Japan, that a landscape is perfect only when water is present.

Very good examples of beautifully developed picturesque valleys can be seen amongst the greater archæan and palæozoic mountains. Here the various degrees of hardness and folding of the rocks offer a very unequal resistance to the weathering and eroding power of the running water.

It only remains now to mention the climate. As I have already pointed out, the Empire of Japan stretches over 30 degrees of latitude. Owing to this considerable length and the great variety in the orographic character of the country, uniformity of climate is out of the question, but to deal with this in detail would occupy too much space. In a word, the climate is much influenced by that of the neighbouring countries, and is modified by the warm and cold currents previously mentioned. The climate of the region from Formosa northward up to the mouth of the Amur River is practically under the control of the monsoons, which are formed by the warm damp south wind in the summer and cold strong north-west, north, and north-east winds in the winter. The Loochoos down to Formosa are sub-tropical and have practically no winter, while the Kuriles, the southern portion of Saghalien, which now again belongs to Japan, and certain parts of Yezo have the climate of Nova Scotia or Iceland. In the winter drifting ice is carried along by the currents and wind in the Kuriles and blocks up harbours, so that navigation is impracticable from November to April. On the northernmost islands of this chain, not until June does the snow disappear from the ground and vegetation then comes to life. Even in the north-east of Hontô, and especially in the so-called deep-snow districts, the snow lies on the ground during the winter some twenty feet deep, so that a whole village is often buried.

The rainfall is very large, and especially in the summer,[1] the air is very damp indeed, except in Hokkaidô (=Yezo and the Kuriles) which is not affected by the monsoon. The winter is dry and fine. The air is clear, the wind refreshing, and the sun bright. The seasons are very distinctly marked and the temperature is fairly even during each season. The annual range of heat and

[1] An example of the rainfall in Tôkyô will be seen in the following table (in mm.) :—

Jan.	Feb.	March	April	May	June	July
55·2	75·1	110·5	128·1	150·0	165·8	131·2

Aug.	Sept.	Oct.	Nov.	Dec.	Year
168·8	203·4	184·8	108·6	53·7	1475·2

cold is, however, much greater than in Britain; *e.g.*, in Tôkyô the mean temperature of the year is 13·8°C, the maximum being 36·6 and the minimum 9·2°.[1]

III.—Comparison and Origin of the Flora.

Under such geographical, geological, and climatic conditions one expects to find a well-developed, varied, and abundant flora. This expectation will be realised, for the traveller meets with beautiful vegetation and an endless variety of plants throughout the country. Up to 1904 some 4,400 species of Cryptogams were recorded, and in the Index of Japanese Plants which has just been completed some 6,000 species of Phanerogams are enumerated,[2] we know, therefore, that there are not less than 10,000 species of plants indigenous to Japan. This number, however, does not include the plants of Saghalien and Corea, which came into the possession of Japan after the above-mentioned index was commenced.[3] An exhaustive survey of plant-species is not yet possible, for new species and varieties are constantly being published.

The flora of Japan belongs to Drude's Eastern Asiatic Region. Although the Empire is surrounded by seas, in the west it is closely connected with Manchuria through Corea, in the north it reaches Kamtschatca by the Kurile Islands, and Alaska through the Aleutian Islands, and also has a connexion with Amurland through Saghalien. On the other hand the Loochoos and Formosa join it to Southern China, the Philippines and the East Indian Islands. Thus, except on the eastern side, it is closely connected with other countries, and their respective floras show many signs of a close relationship with that of Japan.

It is rather difficult to say exactly when the archipelago of Japan separated from the Asiatic Continent, but there is evidence that Japan was connected with the mainland of Asia until a comparatively recent period. Plants indigenous in the eastern parts of Asia are also found in Japan. Teeth and various bones of the mammoth have also been discovered in several parts of the country.

[1] An example of the mean temperature in Tôkyô is as follows (in C.):—

Jan.	Feb.	March	April	May	June	July
2·8	3·6	6·8	12·4	16·6	20·4	24·2

Aug.	Sept.	Oct.	Nov.	Dec.	Year
25·6	22·2	15·8	10·1	5·1	13·8

[2] Matsumura, Index Pl. Japonicarum, 1904—1912. The last volume of this Index includes but a few plants published after 1910.

[3] There are known more than 300 species of higher plants from the Japanese part of Saghalien, while in Corea there are roughly 2,150 species, of which about 200 are endemic. (The latter information was kindly supplied by Dr. T. Nakai, the author of *Flora Koreana*).

The characteristics of the flora of Japan in general are first the abundance of species and varieties, secondly, the presence of a large number of endemic species, thirdly, the proportion of woody plants is remarkably high, and lastly, the presence of tropical and sub-tropical elements throughout the country. Even in Yezo, the large island of North Japan, are found many representatives of southern floras, such as *Picrasma*, *Vitex*, *Rhus*, *Hydrangea*, *Lespedeza*, *Phellodendron*, *Aralia*, *Magnolia*, and others growing together with representatives of the cold flora. In the northern parts of Hontô, *Æsculus*, *Zanthoxylon*, *Ardisia*, *Elæagnus*, *Smilax*, and *Camellia* are often seen. The same or closely allied species have been found in the tertiary strata of the north of Eastern Asia. Probably in the middle of the tertiary period, even Saghalien had a much warmer climate, for at that time *Ginkgo*, *Biota*, *Sequoia*, and *Nilssonia* grew there. When, towards the end of the tertiary period, the greater part of the northern hemisphere was covered with ice, the main island of Japan seems to have suffered very little. Perhaps since the end of the glacial period and the change of climate in the middle diluvial age, Japan has maintained a fairly warm temperature, enabling many plants of warmer climates to survive, while in Saghalien the temperature has been very low, so that this island is unfavourable to plants of the warm temperate region. The arctic plants once compelled by the cold climate of the glacial period to come down southward were consequently left behind when the climate became warmer, but only persist on the summits of the high mountains.

Starting with the flora established in the tertiary period, the migration of arctic plants towards the south and of tropical plants towards the north has caused the present flora to be very complex. The connexion of the country with the northern, north-eastern, south-eastern, and southern parts of the Asiatic continent made paths for arctic and tropical plants into Japan. The interruptions between the various islands are bridged over to some extent by the currents and wind. The introduction of seeds might not have been successful, if the conditions of climate and soil had not been so favourable. Evergreen trees and shrubs and many other tropical plants found their way by degrees towards the north, and became acclimatized—so we may presume—to the colder winter night and contented with comparatively high temperature during the day, and above all the warm and moist atmosphere during the summer, when they can obtain their vital requisites. Those which came

from the north or north-west, where they were accustomed to a severe winter, migrated up the mountains until they obtained the necessary climatic conditions.

Migrations must also have taken place in the post-tertiary period, for the great majority of the volcanoes were built up then, and also the irregularity of the surface of the country was to some extent brought about at this time.

From the results of investigations of the tertiary fossils of Japan, of Amurland, and of N. America, the conclusion may be drawn that the present flora originated in the large common flora of the northern region of the Far East. Its development to its present condition has already been elucidated. One striking feature is that the flora of the N.E. part of Japan bears a close relationship to that of the Atlantic coast of N. America. This was first noticed by Asa Gray a good many years ago. He endeavoured to compare the two floras and showed that more that 60% of Japanese plants grew on the E. coast of N. America, or if not, were represented by closely related species, while only 37% of these can be seen on the W. coast. He accordingly suggested that the close affinity between these floras originated in the tertiary period. Asa Gray's conclusion has been more and more firmly established as further geological evidence has accumulated, and consequently Engler and other geographical botanists have come to the conclusion that these two regions were actually connected, and had a similar climate and similar flora. After the glacial period many plants which migrated towards the south returned northwards and formed the foundation of the present flora of Japan, while in N. America, a change in climate had taken place between that of east and west. While in the west the climate became dry and mild and caused a great alteration in the flora, in the east very little change has taken place, and many old species have been preserved.

It should be borne in mind, however, that the vegetation of Japan, except that of the northern islands, has little actual resemblance to that of N. America. Although the same or closely allied plants occur in both regions, they are not found in the same proportion. For instance, in Japan *Tsuga* forms continuous and almost unbroken forests of great extent on the mountain slopes, above 5,000 feet from sea level, while in eastern N. America this tree is rarely found except scattered in small groves or as single individuals in the deciduous forests. On the other hand, *Picea* and *Abies*, which in America form immense forests almost to the

exclusion of other species, in Central Japan grow singly or in small groves on the lower border of *Tsuga* forests or mingled with broad-leaved trees. In northern Japan and on the high mountains of Hontô, birches are more abundant than they are in the northern forests of America, and the river banks in the north, like those of N. Europe and Siberia, are lined with arborescent willows and alders, which are rare in eastern America, where these genera are usually represented by shrubs. This difference is due to the other dominant plants peculiar to each flora. The nnmber given in Gray's estimation should also be reduced slightly, since he included as natives some Chinese and Corean plants cultivated in Japan. Besides these and some endemic species, we have, as I have already remarked, a great many plants of the boreal region of the old world. For instance, *Asperula odorata* which occurs in Europe but not in America, grows abundantly in North Japan. In South Japan many tropical and sub-tropical elements may be seen. Certain plants growing in the central and southern parts of the country have also a close affinity to those of S. China as well as to those of the Himalayas.

IV.—Regions of Vegetation.

As has already been said, owing to the considerable length of the Empire, we cannot deal with the vegetation collectively, but are bound to divide it into certain regions. It may conveniently be arranged in three divisions mainly based on the climatic conditions:—(1) Northern, (2) Middle, and (3) Southern Regions. The Northern Region extends from the 38th degree of latitude northwards to the Kuriles and Saghalien. We may also include in it the northern part of Corea. The Middle Region is formed of the greater part of Hontô and Shikoku, a small part in the north of Kyûshû, and South Corea. The Southern Region includes the southern parts of the province of Kii and Shikoku, the greater part of Kyûshû, the Bonin Islands, the Loochoos, Formosa, and the Pescadores.

We must note here that within each of these regions there exists a certain degree of difference in the vegetation, according as we consider the northern or the southern portion. The northern part of the Northern Region is represented by the arctic, and the southern part by the sub-arctic, with a few elements of the cold temperate flora. In the northern part of the Middle Region the plants of the cold temperate flora are to be found, and in its southern part those of the warm temperate. The Southern Region

possesses warm temperate and sub-tropical plants in its northern part, and tropical plants in the southern.

V.—Plant-Formations.

In this chapter I intend to deal very briefly with various plant-formations. For the sake of convenience, the above-mentioned three regions are treated separately.

1. Northern Region. The sea-coasts of this region are lined partly with sand-dunes and partly with cliffs. In Hokkaidô, and especially in the Kuriles, sand-dunes are poorly developed. On the sand one generally finds *Amodenia* (*Arenaria*) *peploides* var. *oblongifolia*, *Arabis japonica*, *A. perfoliata*, *Matricaria ambigua*, *Atriplex patula*, *Carex macrocephala*, *C. pumila*, *Elymus mollis*, *Geranium yezoense*, *Inula Pseudo-Arnica*, *Lactuca repens*, *Linaria japonica*, *Lathyrus maritimus*, *Lilium dahuricum*, *Mertensia maritima* subsp. *asiatica*, *Phellopterus litoralis*, *Plantago camtschatica*, *Poa glumaris*, *Salsola soda*, *Thermopsis fabacea*, etc. In the sea we often come across *Phyllospadix Scouleri* and *Zostera pacifica*. Just inside the sand-dunes *Rosa rugosa*, which is very often cultivated in English gardens, forms thickets. Exposed parts of the cliff are often strikingly adorned with quantities of interesting arctic flowers, and even a small patch of rocks may form a beautiful garden. Some of the plants which we see here are as follows :—*Androsace Chamæjasme*, *Artemisia sacrorum*, *A. Schmidtianum*, *Chrysanthemum arcticum*, *Cochlearia oblongifolia*, *Conioselinum camtschaticum*, *Draba borealis*, *Empetrum nigrum*, *Erigeron subsuginosus*, *Fritillaria camtschatcensis*, *Hedysarum obscurum* var. *neglectum*, *Leontopodium kurilense*, *Ligularia sibirica*, *Lloydia alpina*, *Mertensia rivularis* var. *japonica*, *Oxytropis retusa*, *Parnassia palustris*, *Pedicularis venusta* var. *Schmidtii*, *Potentilla megalantha*, *Primula modesta* var. *Fauriæ*, *Rhododendron kamtschaticum*, *Salix arctica*, *Saxifraga bronchialis*, *S. cortusifolia*, *S. reflexa*, *Sedum camtschaticum*, *S. Rhodiola*, *Vaccinium Vitis-Idæa*, and so forth.

The salt-marsh, which is not a rare formation in N. Europe, is very feebly developed. There are only three or four localities known where *Salicornia* is found. But in rather muddy places near the sea, one often comes across the pretty *Glaux maritima* and *Triglochin maritimum*.

The dry hillsides are usually covered with *Miscanthus*, with which various species of *Artemisia*, *Aconitum*, *Convallaria majalis*, *Geranium*, *Hemerocallis Middendorffii*, *Lespedeza*, *Platycodon*, *Rumex*, and

Umbelliferæ. In humid places of the mountain valleys we often find *Artemisia vulgaris*, *Cacalia hastata*, *Lilium cordifolium*, *L. Glehni*, *Petasites japonicus*, *Polygonum sachalinense*, *Urtica platyphylla*, and so on, most of which are very robust.

The *Sphagnum* bog or "Hochmoor," which is not much in evidence in the other regions, is here fairly well developed. The following plants are frequently met with:—*Caltha palustris*, *Carex* spp., *Clematis fusca*, *Cornus suecica*, *Drosera rotundifolia*, *Eleocharis* spp., *Eriophorum alpinum*, *E. vaginatum*, *Gentiana jesoana*, *Ledum palustre* var. *dilatatum*, *Lonicera cœrulea*, *Lycopodium clavatum*, *L. inundatum*, *Lysichiton camtschatcense*, *Molinia cœrulea*, *Myrica Gale* var. *tomentosa*, *Oxycoccus palustris*, *Phalaris arundinacea*, *Scheuchzeria palustris*, *Scirpus* spp., *Trientalis europæa* var. *arctica*, etc. In the early summer when the silky cotton-grass displays its beauty, blue Irises (*I. lævigata* and *I. setosa*) take their part in adorning the swamp. Pretty orchids such as *Arethusa japonica* and *Pogonia japonica*, the blue *Gentiana Thunbergii*, the tall *Viola Langsdorffii*, and the white *Spiræa betulifolia*, present a delightful sight. Tall Umbelliferæ such as *Angelica* and *Heracleum*, which remind us of the scenery of the arctic vegetation, line the margin of the swampy places in the summer, but in the autumn these are replaced by the huge *Senecio palmatus* with yellow flowers, and the deep blue *Gentiana jesoana* is fully open.

In the ponds and lakes one often sees *Hippuris vulgaris*, *Polygonum amphibium*, *Potamogeton natans*, *P. perfoliatus*, with which *Fontinalis*, *Lemna trisulca* and *Utricularia minor* are occasionally associated.

In the deciduous woods, on hillsides, and even on the fairly high mountains, *Sasa paniculata*, *S. kurilensis* and *S. nipponica* are very abundant. These bamboos have comparatively thin culms and broad leaves, and form very dense thickets, under which various shade-loving plants find protection.

The characteristic forest trees are the deciduous oaks (*Q. dentata*, *Q. glandulifera*, and *Q. grosseserrata*), birches (*B. alba*, *B. Ermani*, *B. Maximowiexiana*), cherries (*P. Maximowiezii*, and *P. serrulata*), elm (*U. japonicus*), hornbeam (*C. cordata*), maples (*A. japonicum*, *A. Mayri*, and *A. pictum*), poplars (*P. suaveoleus* and *P. tremula*), and *Cercidiphyllum japonicum*. The last-named is a very peculiar tree, the sole representative of the family Cercidiphyllaceæ. Its general appearance closely resembles that of *Ginkgo*, so that it has often been mistaken for the latter by casual travellers.[1] Various

[1] cf. Hemsley, Ind. Fl. Sin. ii, p. 547; also *Ann. Bot.*, xiv, p. 119.

kinds of *Salix* are very often found in more or less damp places. Conifers are not rare, but comparatively few species are present, e.g., *Abies Mariesii, A. sachalinensis, Juniperus chinensis* var. *procumbens, Larix dahurica, L. kurilensis, Picea ajenensis, P. Glehni,* and *Taxus cuspidata.* Pines are rare except in cultivation. The only wild species is *P. pumila* which is usually three or four feet, occasionally five to seven feet in height, and generally grows on mountain summits. *Thujopsis dolaborata,* one of the finest Conifers, grows to a great size in the southernmost part of this region.

Even in Saghalien and the Kuriles we often meet with several woody climbers, such as *Actinidia arguta, A. Kolomikta, Celastrus articulatus, Hydrangea scandens, Rhus Toxicodendron* var. *radicans, Vitis Thunbergii,* etc., which grow in tropical luxuriance. Not only here, but also in other parts of Japan, we frequently find many woody climbers. Sargent attributed this fact to the abundant undergrowth of bamboos, which cuts off most of the light, and makes the plants climb up the trunks of other trees.

On the high peaks which are not much more than 7,000 feet in altitude, we find many interesting arctic plants such as *Bryanthus* and *Phyllodoce* generally growing on exposed rocks.

The vegetative period of this region is very short. Still, as soon as the spring arrives, everything is quite ready for rapid growth, and before September comes with the keen autumn wind, seeds are set and dispersed.

2. Middle Region. This region is very extensive and mountainous, so that the vegetation is not uniform.

The coasts are beautifully lined with graceful pine trees. *Pinus Thunbergii,* which is well adapted to sandy sterile localities, is the species most often found on the sea shore. The following plants are some of the representatives of the sand-dune plants:—*Amodenia peploides* var. *oblongifolia, Arabis japonica, A. perfoliata, Artemisia Fukudo, Arundo donax, Bœhmeria biloba, B. holosericea, Calystegia Soldanella, Carex macrocephala, C. Pierotii, C. pumila, Cinidium japonicum, Crepis lanceolata, Crinum asiaticum* var. *declinatum, Corydalis platycarpa, Dianthus japonicus, Fimbristylis spathacea, F. velutina, Ischæmum anthephoroides, I. Sieboldii, Lactuca repens, Lathyrus maritimus, Linaria japonica, Lubinia lubinioides, Phellopterus littoralis, Rhaphiolepis japonica, Samolus floribunda, Sedum oryzifolium, Statice japonica, Vitex trifoliata* var. *orata, Wedelia procumbens.* Rocky cliffs are infrequent, nor do they present a gay

appearance as they do in the Northern Region. The species growing in this sort of locality are comparatively few, such as *Chrysanthemum Decaisneanum*, *C. marginatum*, *Cotyledon* spp. *Sedum* spp., *Polystichum falcatum*, and so forth.

The forest trees of this region are of great variety. Evergreen trees occur largely and broad-leaved species are especially numerous. In the spring trees and shrubs with conspicuous flowers such as different kinds of *Azalea*, *Prunus* and *Pyrus* decorate the woods on every hand, and in the autumn the foliage of various deciduous trees displays gorgeous hues. More species of *Pinus* appear in this region, and *Cryptomeria*, one of the most beautiful trees in Japan, flourishes here. The tall bamboos, mostly belonging to the exotic genus *Phyllostachys* add a special feature to the vegetation. They are almost exclusively under cultivation, and form dense groves. The largest of them (*P. edulis*) exceeds 30 feet in height, the base of the culm measuring as much as 10 inches in diameter.

The uncultivated fields, which are called "hara" in general, are usually covered with a dense growth of *Miscanthus* and other grasses, amongst which grow small shrubs and thousands of herbaceous plants, including the fine *Lilium auratum*, that prefer dry sunny situations.

This middle region contains the huge mountain ranges with perpetual snow lying in the gulleys, of which I have already spoken. The flora of these mountains generally presents zones of different vegetation, as we ascend from below to the summit.

Taking Mount Fuji, which is the highest volcano in Japan, and is moreover the world-famous "peerless mountain", as a type, we shall find the mountain-flora of a temperate country. This peak stands practically on a plain, and if one likes, one can start climbing from the very seashore. Supposing we take a village at the southern base of the mountain as a starting point, then we shall ascend, first of all, a long gentle slope. This is composed of lava and cinders, and is almost useless for cultivation. Various sorts of grasses, *Rubi*, wild roses, and bracken cover this wide area, and small shrubs and trees grow in scattered spots. In the summer thousands of herbaceous plants with yellow, pink, blue, white or purple flowers convert the wilderness into a splendid flower garden, where one often comes across many a gorgeous butterfly. Small patches of alluvial soil deposited by the action of water are seen here and there. In such places many interesting trees such as *Abies*

firma, *Acer* spp., *Castanea sativa*, *Cephalotaxus*, *Cinnamomum Camphora*, *C. pedunculatum*, *Cryptomeria japonica*, *Diospyros Kaki*, *Eurya japonica*, *Larix leptolepis*, *Listea aciculata*, *L. glauca*, *Pasania cuspidata* and *Quercus* spp. are to be found, partly wild and partly planted.

At the 3,000 feet level the basal zone which we have just passed, begins to show a transition to the tree zone. The tree zone may be divided into the deciduous tree belt and the conifer belt, the former taking the lower part and the latter occupying the upper portion. The broad-leaved trees growing here include the following:—*Acer*, *Alnus*, *Betula*, *Carpinus*, *Cercidiphyllum*, *Cornus*, *Corylus*, *Euptelea*, *Euonymus*, *Hydrangea*, *Quercus*, *Stephanandra*, *Viburnum*. Very many shade loving plants form the undergrowth. In the conifer belt, *Abies firma* appears first, and this is followed by *Larix*, *Picea*, *Tsuga*, and other species of *Abies*. Mosses and liverworts form a thick cushion on rocks and trunks, and with these occur a number of interesting ferns and orchids.

When we reach the 6,000 feet level, the gradient becomes much steeper, and trees are less abundant. The mountain ash, *Rhododendron*, *Alnus* spp., stunted birches, shrubby *Spiræa*, dwarf willows and various ericaceous shrubs remind us that we are reaching the shrub zone. The flowers we meet with here are mostly of alpine character. Species of such genera as *Adenophora*, *Arabis*, *Artemisia*, *Astragalus*, *Clematis*, *Geranium*, *Patrinia*, *Polygonum*, *Stellaria*, and *Thalictrum* are quite different from their congeners growing down below.

The zone between 7,500 feet to 10,000 feet from sea level belongs to the Alpine region. Plants growing in this zone are typically alpine and arctic. *Arabis serrata*, *Artemisia pedunculosa*, *Astragalus membranaceus*, *Clematis alpina*, *Hedysarum esculentum*, *Polygonum cuspidatum* forma *colorans*, *Stellaria florida* var. *angustifolia*, *Vaccinium Vitis-Idæa* are the plants which commonly occur here.

Above this up to the summit, which is about 12,450 feet above sea-level, is the Lichen zone, where one comes across various lichens such as *Cetraria islandica* forma *angustifolia*, *Cladonia rangiferina*, *Rhizocarpon geographicum* and *Stereocaulon octomerum*. Here and there those plants which we have seen in the Alpine zone grow in crevices of the lava, but they do not thrive as they do some way further down.

Practically the whole area of the summit is occupied by a large crater not far short of 2,000 feet in diameter, which is surrounded by a series of small rugged peaks. Two springs of very pure cold water supply the demands of crowds of mountaineers.

The Alpine zone of Mount Fuji does not contain many plants, though there are a few things only known from this mountain. On the other mountains of Central Japan, which form the back-bone of the main island, and are often called the Japanese Alps, the Alpine vegetation is very well developed. On these mountains a creeping pine, *Pinus pumila* which also occurs in Siberia, appears in the shrub zone, and extends to the Alpine zone. The thickets of this pine are very troublesome to cross, but under their shade various interesting plants are found, *e.g.*, *Coptis trifolia*, *Fritillaria camtschatcensis*, *Linnæa borealis*, *Lycopodium alpinum*, *L. Selago* var. *appressum*, *Listera cordata* and other orchids, *Rubus pedatus*, *Viola biflora*, *V. crassa*, and so forth. Many arctic plants which occur on the rocky cliffs of the Kuriles can also be found in the Alpine zone of these mountains. One of the most attractive things is *Dicentra pusilla*. This plant is about a span high, with much dissected, intensely glaucous leaves, and a terminal raceme bearing some half-a-dozen large pink flowers. A beautiful sight is a carpet made up of the crimson flowers of *Primula cuneifolia* with white patches of *Anemone narcissiflora*. Mosaics of the crimson *Geranium yezoense* var. *nipponicum*, the golden-yellow *Ranunculus acris* var. *Steveni* and *Trollius patulus*, and the blue *Aquilegia siberica* var. *flabellata* are another sight of the Alpine zone. On the rocks we occasionally find *Campanula lasiocarpa*, *C. pilosa* var. *dasyantha*, *Diapensia lapponica* var. *obovata*, *Empetrum nigrum*, *Eritrichium nipponicum*, *Geum calthaefolium* var. *dilatatum*, *Hypericum camtschaticum*, *Lloydia alpina*, *Saxifraga bronchialis* var. *cherlerioides*, *Sedum Rhodiola* var. *Tachiroei*, and so on. In the crevices of the rocks the very peculiar looking *Cassiope lycopodioides* grows, while its congener *C. Stellariana* prefers a moist place. *Dryas* is very rare, and is known only from four or five localities, but it is replaced by a member of the same family, namely *Geum dryadoides* which has white flowers and bearded achenes. The species of *Ranunculus* with white flowers are totally unknown from the Japanese Alps, while *Soldanella* is replaced by a member of the Diapensiaceæ called *Shortia soldanelloides*. Neither *Cyclamen* nor *Sempervivum* grow in any part of Japan. One of the rare and interesting plants is *Anemone Taraoi*,[1] with a pale

[1] For a description, see *Journ. Bot.*, 1910, p. 266.

yellow flower, which though it has a similar appearance to *A. sulphurea*, belongs to a different subgenus. This plant is endemic to Japan and occurs only on the summits of a few high mountains and in the Kurile Islands. When, in the late summer or early autumn, the frost has made the leaves of *Arctous alpina* bright red, a mountaineer will enjoy ripe fruits of various species of *Vaccinium*, *Prunus*, *Lonicera*, and *Empetrum*. In rather dry sandy places one often finds species of *Adenophora*, *Arnica*, *Draba*, *Euphrasia*, *Gentiana Loiseleuria*, *Oxytropis*, *Potentilla*, and some grasses such as *Deschampsia* and *Festuca*, while in humid localities *Alchemilla*, *Fauria*, *Pedicularis*, *Phyllodoce*, *Sibbaldia*, *Swertia*, *Tofieldia*, and *Veratrum* are to be found. The ferns growing on the rocks are few, but elegant, and include *Asplenium viride*, *Cryptogramme crispa*, *Polystichum Lachenense* and *Woodsia ilvensis*. While most of these ferns occur in Europe, the *Polystichum* is only known from the Himalayas. *Botrychium Lunaria*, not at all uncommon in Europe, is comparatively rare in Japan, and *B. lanceolatum* is perhaps the rarest. A good many new species of plants have been discovered and described from the Japanese Alps, while many known species have been found and added to the flora. On the whole the Alpine flora of Japan is mostly composed of arctic plants, some of which are not seen on the European Alps.

Finally the aquatic vegetation of the middle region may be mentioned. There is a great diversity in the representatives of aquatic plants. The commonest genera which we find in nearly every pond, ditch, or lake are perhaps as follows:—*Alisma*, *Ceratophyllum*, *Hydrilla*, *Hydrocharis*, *Lemna*, *Monocharia*, *Myriophyllum*, *Nuphar*, *Nymphaea*, *Ottelia*, *Phragmitis*, *Potamogeton*, *Rotala*, *Sagittaria*, *Scirpus*, *Trapa*, *Typha*, *Utricularia*, *Vallisneria* and *Zizania*. Besides these flowering plants, water ferns such as *Azolla*, *Marsilia*, and *Salvinia* occur in the stagnant water. *Isoetes japonica*, which is one of the largest species of this genus, is to be met with in running water in certain places.

3. Southern Region. We will now pass to the Southern Region, where, even at its northern limit, Kyûshû, the vegetation is quite sub-tropical. Particularly on the sea-coasts, which are washed by the warm current, various Indo-Malayan strand plants are to be met with. In the Loochoos, *Bruguiera gymnorhiza* forms the mangrove-forest in the tidal estuaries. Well-developed mangrove-forests are to be seen in Formosa, which are composed of

Avicennia officinalis, Kandelia Rheedii, and *Rhizophora mucronata.* In such marshy places one finds such plants as *Halophylla, Scævola,* and *Suæda australis.* On the sandy beach we often get *Barringtonia* spp., *Cassytha filiformis, Ipomæa biloba, Pandanus* spp., *Peperomia portulacoides, Vigna lutea* and so forth. Various palms belonging to such genera as *Arenga, Livingstonia, Trachycarpus,* and so on, flourish in the Region.

This is really a region of *Ficus,* with which broad-leaved evergreen trees and shrubs such as various Lauraceæ, *Quercus, Hibiscus, Myrica rubra,* etc. are found. On their branches a great many epiphytic orchids, lycopods and ferns, and sometimes parasites such as *Loranthus* spp. and *Viscum japonicum* are found. In the dense moist forests many tropical ferns such as *Allantodia javanica, Alsophila,* spp., *Angiopteris evecta, Cyathea, Dicksonia, Gleichenia* spp., *Osmunda javanica, Pteris quadriaurita, P. wallichiana* flourish. Amongst other woody climbers I may mention the occurence of *Bauhinia japonica* in Kyûshû. In the Loochoos we get more tropical plants such as *Garcinia, Pinus luchuensis, Terminalis Katappa* and others. The famous *Cycas revoluta* thrives very well in these islands, and from its pith a sago is prepared. Various interesting orchids and ferns including *Helminthostachys zeylanica* are also to be met with.

If we pass over the Loochoos and come to Formosa, the vegetation is typically tropical. Although the climate is not uniform throughout the island, huge trees, thick bushes, dense forests with a great number of woody climbers can be found everywhere. In the mountain valleys we frequently come across *Cinnamonum camphora,* from which the camphor of commerce is obtained, reaching huge dimensions. *Macuna gigantea* and *Pusætha scandens,* both famous for their tremendous legumes, other climbers such as the Lotung, and gigantic bamboos, tall tree ferns, palms, and the wild *Musa* grow in the forests and on mountain-slopes. If we go higher up on the mountains which occupy the greater part of the island, we shall see conifers at an elevation of about 6,000 feet above sea-level. *Chamæcyparis formosensis, Cunninghamia Konishii, Picea morrisonicola,* and *Pinus formosana* are some of the interesting species, and are only known from this island. A few years ago a new genus of conifer was discovered amongst the mountains, about 6–8,000 feet above the sea. The external appearance of this tree is somewhat similar to that of *Cryptomeria,* so that people thought at first that they had found a

wild *Cryptomeria*, until the cone was obtained and closely examined. Then the plant proved to be a new genus and was accordingly named *Taiwania cryptomerioides* in honour of this beautiful island. The systematic position of this genus was suggested to be between *Athrotaxis* and *Cunninghamia;* further investigations, both anatomical and cytological, are much to be desired.

Higher up on the mountains we first get the shrub-zone and then at an elevation of 12,000 feet and upwards various plants of alpine and arctic character, such as *Arabis*, *Artemisia*, *Cerastium*, *Deschampsia*, *Festuca*, *Fragaria*, *Gentiana*, *Gnaphalium*, *Leontopodium*, *Luzula*, *Potentilla*, *Shortia*, *Sibbaldia*, *Trisetum subspicatum*, and so forth.

If we go down to the southernmost part of the island, we shall everywhere meet with nothing but real tropical plants, and the vegetation shows a close relationship to that of the Philippines, India, and Java. Certain elements belonging to Cochin-China and of southern China will also be detected.

Roughly speaking, there are some 2,500 species (belonging to some 770 genera) of higher plants known, 17% of which are endemic; and many more will be discovered in the future in this island which promises so much to the enthusiastic botanist.

VI.—Cultivated Crops.

A few words may perhaps be added on this subject. The most important plant is undoubtedly the rice-plant, *Oryza sativa*, with a great many cultivated varieties and races. The plant is grown throughout the country with the exception of Saghalien and the Kuriles. Particularly in Central and S.W. Japan, every possible piece of land is converted into rice-fields, which present a very striking feature to the eye familiar only with European scenery. A rice-field is, in a word, a muddy swamp divided up by low narrow banks into more or less square areas. The plant is raised in the nursery and seedlings of about a span high are transplanted from this into the rice-field proper. In the summer the rice-field is of a delightful green colour; in the autumn it turns somewhat golden, as the grain ripens and the plant withers. In the winter, after the harvest, the rice-field looks quite desolate, but often furnishes the best shooting-ground for snipe and other game-birds. Sometimes the rice-plant is also grown in dry fields where water is not available.

In Saghalien and the Kuriles, the temperature is very low during more than half the year, so that cultivation is hardly to be

hoped for. The vegetation of these districts is little touched by human hands, so that the original features are exceedingly well seen.

In Yezo, except perhaps its eastern parts, the temperature rises considerably in the summer, so that various sorts of grain and vegetables are produced, and especially excellent varieties of apple. The cultivation of the hop and flax, which meets with considerable success, may also be mentioned.

In the Middle Region, plains and small hills are cultivated with rice, other grains, beans, peas, cucumber, egg-plant, radishes, turnips, mustard, *Lagenaria, Colocasia antiquorum*, potatoes, sweet potatoes, and so forth. Besides these vegetables one often comes across the cotton-plant, hemp, tobacco-plant, and mulberry, the last of which is utilized for sericulture. Various fruit-trees such as apricot, fig-tree, peach, pear, persimmon, orange, vine, and *Eriobotrya* are also grown. Nor must I omit to mention the tea-plant, and paper mulberry and *Edgeworthia* for paper manufacture. Various species of the bamboo, *Phyllostachys*, which, as already said, form a peculiar feature in the warmer parts of Japan and were probably introduced from China at an early period, yield valuable material for various purposes. Fences, pegs, baskets, arrows, trellis-work, hoops for barrels, shafts of umbrellas, cages, and fishing rods can be made out of the culm, while the sheath of the young shoot is useful for wrapping or for making hats or sandals. There are a good many species of bamboo, belonging to *Arundinaria*, *Bambusa*, and *Sasa*, used for similar purposes, or much valued as ornamental plants. A species of *Dendrocalamus*, from which a kind of paper can be manufactured, grows in Formosa.

As a matter of course sub-tropical and tropical crops are grown in the Southern Region. In addition to those mentioned above in the Middle Region, there are such plants as bananas, coco-nut, pine-apple, and sugar-cane. *Musa luchuensis* yields a fibre of good quality, while an excellent kind of hat can be made out of the leaves of a screwpine. *Tetrapanax papyrifera*, from the pith of which the so-called rice-paper is prepared, grows in Formosa.

VII.—Introduced and Garden Plants.

In this last chapter I may perhaps deal briefly with gardening and garden plants.

Gardening must have been introduced from China together with other arts and especially with Buddhism. Buddhist priests may have been the first to construct gardens after the Chinese patterns,

which was greatly modified in later years. So far as I know, one of the famous gardens, designed some 500 years ago, still exists.

Generally speaking, the gardens are very different from European ones. Geometrical carpet bedding and lawns are quite unknown, and beds are used only in the nursery. Rather different from the original Chinese gardens, which are more artificial and Gothic, the Japanese gardens are miniatures of natural landscape. Generally, there is a small hill or two, a pond, a bridge, and a few stone lanterns. This is copied (very badly) on a small scale and exhibited at the Temple show every year. Trees and shrubs are mostly used, and comparatively few herbaceous plants are grown. Pines and *Chamæcyparis* are indispensable. Except *Abies firma*, which is hardy in the lowlands, other species of this genus and *Picea* are hardly ever seen, while a dwarf variety of *Taxus cuspidata* and *Juniperus chinensis* are sometimes used. Broad-leaved evergreen trees and shrubs are mixed with deciduous plants. Half-a-dozen species of *Prunus* are planted for the sake of their flowers, while a great many varieties of *Acer palmatum* and other species of maple are grown for their foliage. Ferns are usually neglected except for a few hardy species. Amongst shrubs many kinds of *Azalea*, with *Cydonia*, *Nandina*, and *Pyrus floribunda* are favourites, while *Wistaria* is often planted over a pond. Stones and rocks of different colour and shape are always placed in certain definite positions, and sometimes even a small cascade is reproduced falling over a rock. There are several types of gardening, the principles of which are not very easily understood; some trees, shrubs, and stones should occupy a certain position, trees should have certain ramifications, and certain shrubs should be trimmed in definite ways.

In some cases, a landscape garden is skilfully reproduced in a box or in a pot. One of the best examples which was transferred from the Japan-British Exhibition can be seen in Battersea Park, London. For this purpose the plants used must necessarily be small, but perfect in style and shape.

The dwarf pot trees, which appear somewhat mysterious, even to a scientific eye, may also have been introduced from China. The art has been improved with great skill. Not only arboreal plants, but also various other evergreen plants such as *Acorus gramineus*, *Rhodea japonica*, and even *Psilotum triquetrum* became material for pot cultivation. Some are grown for their flowers, others for fruit, or foliage. In some years variegated leaves of any plant are much valued, in other years *Chamæcyparis* is in fashion, and so forth,

Curiosity drove people into little explored parts of the country to discover curious or unusual plants for this purpose. Also, very many plants were imported from China and Corea or even from the tropics. The introduction of foreign plants took place not only in recent years, but in ancient times for economic, pharmaceutical, and other purposes. *Cryptomeria japonica,* for instance, which is so widely cultivated all over the country, is said to have been imported from Corea in prehistoric times. Rice and various other grains must have been brought by our ancestors from somewhere abroad. History tells us that the orange, or at any rate a kind of orange, was imported for the first time in the year 70 A.D. The Corean medical art was introduced into Japan in 510, and with this came also pharmaceutical botany. In 701 a physic garden was established, and medical botany was taught there. Afterwards very many plants possessing medical value were introduced from China and Corea, and in later years many economic and garden plants also. Sometimes the introduction was made quite by chance, *e.g.*, in 799 a foreigner is said to have arrived in Central Japan, having drifted ashore on the waves, and he brought with him some seeds of the cotton-plant.

These introduced plants were not always indigenous to China or Corea. The Chinese imported various plants into their own country from their southern and western neighbours ; *e.g.*, according to the history of the Han, the Chinese General Chang K'ieng who was despatched about 139 B.C. by the Emperor Wu on a diplomatic mission to a neighbour living to the north-west of China, brought back the vine from western Asia about 120 B.C. After the discovery of America, very many American plants were introduced by the Spaniards and Portuguese into the Philippines and the East Indian Archipelago. Their cultivation spread rapidly over the neighbouring parts of the Old World, and they found their way also into China. These plants may possibly have been imported into Japan directly or through China, and throve there equally well with the indigenous forms.

The first European who came over to Japan and made a botanical collection was Andreas Cleyer. He came with a Dutch Ambassador about 1675, and stayed in Western Japan four years. Afterwards he published a book containing illustrations of 1,360 species of plants. Then George Meister who knew Cleyer arrived in Japan in a similar manner, and published in 1692 an account of his journeys and observations. Just after him, in 1690, Engelbert

Kaempfer reached Japan and stayed three years. He was the first to illustrate *Ginkgo* in his book published in 1712. After some ninety years, Thunberg who was a pupil of Linnaeus came over to Japan, studied the plants and published his *Flora Japonica* in 1784. He also published an account of his journeys and illustrations of some Japanese plants. I am not quite certain if these people brought back seeds or plants from Japan, but there is no doubt about Von Siebold who came over some forty years later, and took a few living animals and plants away with him.

Robert Fortune, who paid repeated visits to China during eighteen years from 1843, sailed to Japan in 1860 and again in 1861.[1] He saw a number of interesting plants there and introduced several garden plants. About the same time John Gould Veitch went over to Japan for the purpose of obtaining garden plants, and introduced a great many plants into English gardens in 1861. Amongst others the following few are perhaps worthy of note:—*Adiantum Veitchii* (=*A. monochlamys.*), *Ampelopsis Veitchii* (=*Parthenocissus tricuspidata*), *Abies Veitchii*, *A. Alcockiana*, *Cryptomeria japonica* var. *elegans*, *Lilium auratum*, *Picea ajanensis* var. *microcarpa*, *Polypodium Veitchii*, *Primula cortusoides* var. *elegans* (=*P. Sieboldii*), *Selaginella involvens* var. *Veitchii*.

Messrs. Standish and Noble of Bagshot Nursery were the first to cultivate the new Chinese plants discovered by Fortune. They also received the following Japanese plants obtained by that distinguished collector:—*Aucuba japonica*, *Deutzia crenata*, *Tricyrtis hirta*, etc.

J. G. Veitch was followed by Maries who also collected many dried specimens which are now preserved at Kew, and I have had an opportunity of examining and naming some of them.

These people saw in Japan very many interesting and curious plants and certainly thought all of them were indigenous to Japan, and a number of the new species were named "japonica." In fact some of these are not true natives of Japan, but are merely cultivated in the gardens. For instance, *Cydonia japonica*, generally known under the name of "japonica" in this country, is of Chinese origin. *Eriobotrya japonica* which is so much grown on the northern coasts of the Mediterraneans, is probably not a native of Japan. *Mahonia japonica* is another plant, which was described from a specimen grown in a Japanese garden, was introduced into

[1] The narratives of his journey were published under the title of "Notes on the Botany of Japan" in *Gard. Chron.*, 1861, pp. 145, 312, 385, 456, 576, 737.

Japan in 1684 probably from China, where until to-day no true *M. japonica* has been collected, but an allied plant occurs, *M. Bealei*, which has been taken for the other one in this country. The beautiful garden Chrysanthemum, which is the national flower of Japan, was certainly introduced from China, yet the wild form, the original of the garden variety, grows in the south-western parts of Japan. Nowadays a great number of European and American plants are introduced into Japanese gardens, while quantities of Japanese plants are exported to foreign countries and especially to England, where it always gives me the intensest joy to see the plants of my native land.

THE ECOLOGY OF *CALLUNA VULGARIS.*

By M. Cheveley Rayner, B.Sc.,

(Lecturer in Botany, University College, Reading).

[Plate III and Two Text-Figures].

THE Ling (*Calluna vulgaris*) is usually recorded as forming definite heath communities, in competition with other plants, only on poor and often acid soils, such as those which occur on Bagshot sands, or less typically on the washed-out soils sometimes found overlying limestone and chalk.

A somewhat anomalous distribution of *Calluna* on parts of the chalk downs of Berkshire and Wiltshire has been described in a previous communication.[1]

In that paper it was recorded that sporadic communities of this plant occur on the higher parts of the downs, forming patches of typical heath vegetation quite different in character from the so-called "chalk heath" of the South Downs and elsewhere.

The distribution of these communities is roughly determined by the overlying deposits of clay-with-flints, which give rise in this neighbourhood to fertile loamy soils, with a low percentage of calcium carbonate. The soil in question has the appearance of a

[1] Rayner, M. C., and Jones, W. N. "Preliminary Observations on the Ecology of *Calluna vulgaris* on the Wiltshire and Berkshire Downs." New Phytologist, Vol. X, 1911, p. 227.

fertile loam, and the conditions generally give the impression that the heath flora has become established on the more fertile soils of the area, in competition with the surrounding vegetation.

Mechanical and chemical analyses support this view and indicate that the soil monopolized by *Calluna* is in every respect a good fertile loam with a high percentage of available mineral matter (*loc. cit.*, pp. 236, 237).

A low percentage of calcium carbonate excepted, there is no evident factor to account for the successful competition of the heather; the soil reaction is neutral, and the only feature of note chemically is the rather high ratio of magnesia to lime.

With regard to the significance of this ratio as it affects plant growth, there is at present a conflict of opinion and the evidence adduced by different observers is somewhat contradictory.

Two distinct problems were suggested as a result of these observations :—

(i.) The nature of the soil conditions which allows *Calluna* to compete successfully with other plants on small areas of fertile soil.

(ii.) The significance of calcium carbonate as a factor determining the spread of *Calluna* from those sharply defined areas to the surrounding "down" soil.

These problems do not appear to be capable of explanation in terms of current hypotheses, nor do these hypotheses throw clear light on the causes which determine the calcicole and calcifuge habit exhibited in varying degrees by so many plants.

The present investigation was undertaken primarily in order to study the biological significance of the sharp delimitation of *Calluna* under the conditions described, and secondarily, in order to ascertain whether the facts obtained in the course of the investigation might throw light on the larger question of the ecology of calcicole and calcifuge plants in general.

(*a*). Experimental work was begun with two objectives in view. Sand and water cultures were grown in the hope of obtaining evidence as to the effect of alteration in the proportions of lime and magnesia in the culture solutions.

Water culture experiments carried on continuously for twelve months pointed to the conclusion that further work in this direction was premature at this stage of the enquiry and unlikely to lead to definite results. They were therefore discontinued: the results obtained are briefly summarized at the end of this paper.

(*b*). Pot cultures were started using seed and fresh soils from the field, with a view to detailed observations on the behaviour of seeds and seedings under experimental soil conditions. Full analyses of the soils are available and have been recorded in a previous paper (*loc. cit.*). In these analyses the soils are referred to as "heather area" and "soil over chalk" respectively. For the sake of brevity they will be known as "heather" soil and "chalk" soil in the present paper. The former is apparently a good fertile loam although the percentage of calcium carbonate is low: the latter is a typical chalk-down soil containing 41·8% calcium carbonate.

It is convenient to deal with the results of these cultures under two heads:—(A) Germination, (B) Growth.

A. *Germination.* Seed was collected in the capsules during October, dried in the laboratory at air temperature and stored in paper bags. When required it was rubbed down, sieved, and the seed picked out by hand.

The seed is very small, with a rough testa, abundant oily endosperm and a minute straight embryo. Sowings were made in pots of fresh soil, under glass, using approximately the same number of seeds per pot, and records kept of the rate of germination, the number of seedlings, and the growth and condition of the roots and shoots at successive stages.

In the autumn, germination begins 25—30 days after sowing, and is usually rather slow and irregular. In the spring it takes place more uniformly, 16—19 days after sowing.

In "heather" soil, seeds germinate at the same rate and exhibit about the same germination capacity as on blotting paper in a germinator. As compared with this, the rate of germination is greatly retarded and the germination capacity markedly lowered in the "chalk" soil. A majority of the seeds do not germinate. Germination of the remainder is delayed—seedlings first appearing after two or three months and then in very small numbers. Seeds continue to germinate irregularly for six months or longer, but the total germination capacity is extremely low as compared with the controls.

In order to compare the behaviour of *Calluna* seed in this respect with that of other plants, sowings were made, in the two soils, of Foxglove (*Digitalis purpurea*) as a representative calcifuge, and of Kidney Vetch (*Anthyllis vulneraria*) as a calcicole. The latter plant is abundant on the down soil in the field.

In each case germination is simultaneous and the germination capacity similar in the two soils.

The phenomenon of retarded germination in a soil unfavourable to the growth of the plant does not appear, therefore, to be one which occurs generally in the case of calcicole and calcifuge plants.

Heating *Calluna* seed for some hours at a temperature of 67°C. to 70°C. hastens germination, the acceleration so produced being more marked in the autumn.

Seed so treated germinates more evenly and about seven days sooner than unheated seed.

Heating for a longer period, *e.g.*, twenty hours at 70°C. affects the germination capacity adversely, but not the vitality or rate of germination of those seeds which germinate.

No difference can be detected in the behaviour of seeds germinated at once after heating and those kept for several weeks before sowing.

Partial sterilization of the soil, by treatment with vapour of carbon bisulphide and by heat, gives somewhat irregular germination results, which are summarized in Table I. The soil for these experiments was treated as follows:—

Small quantities of soil were spread out in carbon bisulphide vapour for three or four days, then exposed freely to the air for several days, placed in small sterile pots and watered with distilled water. Other samples of soil were subjected to intermittent heating at 92°C. and 98°C. on five successive days, moistening with sterile water between each heating. The seed used for these experiments was in all cases untreated, and control seeds of oat placed in the pots germinated normally.

Reference to the tabulated records shows that the behaviour of the seedlings when the *unfavourable* soil is subjected to partial sterilization is noteworthy and in striking contrast with their reaction to the same soil untreated. The germination capacity remains low as in untreated soil, but the rate of germination is accelerated. The resulting seedlings develop a larger and more normal root system (Plate III, Fig. 1d).

B. *Growth.* Seedlings of *Calluna* are small and slow-growing. The primary root elongates slowly, but soon after germination several adventitious roots grow out in rapid succession from a thickening at the base of the hypocotyl.

The roots are almost transparent and provide beautiful material for observing the details of root structure. Root hairs are absent; the cortex consists of a few cell rows only, and the whole root is extremely slender and delicate.

TABLE I.—GERMINATION OF *CALLUNA* SEED.

			Seedlings First Appear.	Number (Approximate).	Remarks.
Moist Air.	*Autumn.*	1 Control (seed untreated)	... 28 days ...	42%	Germination of untreated seed is very irregular in autumn.
		2 Ditto...	... 26 ,, ...		
		3 (Seed heated 4 hours at 67°C.)	... 17 ,, ...	50%	Germination more uniform. A majority of the seeds germinated simultaneously.
	Spring.	4 Control (seed untreated)	... 16 ,, ...	2 Seedlings ...	In the spring acceleration is less marked, but germination takes place more uniformly in the case of heated seed.
		5 (Seed heated 4 hours at 70°C.)	... 16 ,, ...	40%	
Untreated Soil.	*Late Autumn.*	*Heather Soil* (1)	... 23 days ...	100 seedlings	Approximately the same number of seeds sown in each case (250-300). In pots 1 and 2 seedlings appeared uniformly in pot, and majority ultimately germinated. In pots 3 and 4, 15-20 seedlings had appeared at the end of 6 months and represented the total germination capacity.
		,, ,, (2)	... 21 ,, ...	50 ,,	
		Chalk Soil (3)	... 68 ,, ...	5 ,,	
		,, ,, (4)	... 112 ,, ...	3 ,,	
Partially Sterilized Soil.	*Heather Soil.*	Control	... 53 days ...	Numerous seedlings	Germination extremely slow, possibly owing to spell of very cold damp weather.
		CS_2 Vapour	... 94 ,, ...	4 seedlings ...	Result not confirmed.
		Heated	... 50 ,, ...	Numerous ...	More numerous and rather more vigorous than control.
	Chalk Soil.	Control	... 112 days ...	2 seedlings ...	Total germination capacity not materially affected by either treatment; remains very low.
		CS_2 Vapour	... 50 ,, ...	2 ,, ...	
		Heated	... 55 ,, ...	1 ,, ...	

From the earliest stages, whether growing in moist air or in soil, the roots are infected with an endotrophic mycorhiza. Branched hyphæ project from the surface and many of the cortical cells contain the characteristic "knots" of mycelium.

The plumule is undeveloped in the resting embryo and growth of the shoot is slow, especially in the early stages.

In the "heather" soil seedlings grow normally; the leaves are bright green and a vigorous much-branched root-system is rapidly formed (Plate III, Fig. 1a).

Partial sterilization of this soil by carbon bisulphide, as described above (p. 62), gives an impetus to vegetative growth and the seedlings, for a time, compare favourably with the controls. Examined microscopically the roots of such seedlings are cleaner and fungal infection is rather less conspicuous (Plate III, Fig. 1b).

In the "chalk" soil, growth is practically inhibited.

The few seedlings which germinate remain in the seed-leaf stage for many months. Sometimes no other leaves are formed: those which do appear are small and chlorotic, and the whole shoot usually becomes bright red in colour. Root growth is almost completely checked; many lateral roots begin to develop, but their tips are strongly recurved and often show brownish discoloration (Plate III, Fig. 1c).

Seedlings may remain in this condition for months, making repeated but ineffectual efforts to form an adequate root system: if transplanted to the other soil, they at once recover and grow normally. Examined microscopically, these abnormal roots are remarkable, not only for the retarded growth and peculiar curvatures which they exhibit, but for the association with them of dense colonies of bacteria. The latter are especially conspicuous about the tips, which are usually invested with dense bacterial sheaths.

Bacteria are also abundant in and about many of the cortical cells and around the apices of young emerging lateral roots (Plate III, Fig. 2b, Fig. 3).

In "chalk" soil sterilized by either of the methods described on page 62 root development is more normal for a time. Bacterial growth appears to be retarded; a more normal root system is developed and reddening of the shoot takes place rather more slowly. This improvement, however, is temporary, and eventually the same symptoms appear as in roots in untreated soil (Plate III, Fig. 1d). In all these abnormal roots, mycelium, though present,

is scanty in amount, few hyphæ project from the root and they are often crowded with bacteria.

The effect of watering seedlings growing in "heather" soil with a watery extract of "chalk" soil has been tried, with the following results:—

After four months of regular treatment seedlings in small pots do not differ markedly from the controls. After six to seven months treatment, seven out of eight seedlings so treated begin to show signs of injury. Growth was stunted, the foliage yellowish and discoloured, and the leaves dead on some of the older shoots (Plate III, Fig 4).

Examined microscopically, the roots of these seedlings show in a rather less marked degree the same peculiarities as have been already described for roots growing in "chalk" soil. Root growth is evidently checked, the tips show marked curvatures and are often invested with a dense mantle of bacteria. Mycorhizal growth is poorly developed and the general appearance of the roots quite characteristic.

Seedlings growing in larger pots responded to similar treatment much more slowly. After treatment for the same length of time, the growth and general condition of the shoot was practically unaffected.

Many of the root-tips, however, when examined microscopically, showed characteristic association of the mycelium with bacteria, the relations of the hyphæ with the latter being much more evident in such early stages than they are later when the tip has become invested in a dense sheath of bacterial growth.

Other seedlings growing in "chalk" soil were watered with an extract of "heather" soil prepared similarly to that used in the last experiment. This experiment was begun shortly after germination, before the ill effects of the unfavourable soil conditions had become marked, and was continued for six months. At the end of that period the controls—watered with distilled water—were dead; the seedlings in the three pots under treatment were alive; the characteristic purpling of the leaves had appeared, but most of the plants had made four to six leaves on the main axis.

The change in the root system was more remarkable and is shown in Plate III, Fig. 5.

As is evident from a comparison of this photograph with that of the seedlings shown in Plate III, Fig. 1c, the root system is many times larger than that of a seedling from untreated soil,

During part of the time occupied by the experiment, growth of the roots had apparently been almost normal and resulted in the formation of a more fully developed root system.

Several points of interest are suggested by these observations:

(i). Since the unfavourable and favourable soil conditions respectively can be supplied in a filtered, unboiled soil extract, they are either of a chemical or biological nature.

(ii). If the conditions be biological, and the injurious effect can be produced by supplying an organism present in the unfavourable soil simultaneously with the conditions which favour its growth, all the plants so treated might fairly be expected to behave in the same way.

Unfavourable symptoms appear, however, much more slowly in plants growing in large pots, thereby suggesting that the unfavourable factor is chemical in nature and that as soon as a certain concentration in the soil is reached, an unheathy condition of the roots is induced owing to disturbance of their normal relations with the micro-organisms present,—a view confirmed by the results of the treatment when an extract of "heather" soil is used for watering seedlings growing in "chalk" soil.

Whether the unfavourable effect is a *direct* result of the bacterial colonies which beset the roots, or whether it is *indirect* and due to the effect of these colonies on the micorhizal fungus, remains an open question, as does also the important point as to whether the pathogenic effect of the bacteria is dependent on a change in the chemical condition of the soil, the organism being present in both cases, or whether the latter is peculiar to the soil on chalk.

This experimental work, combined with examination of the roots of large numbers of seedlings grown under different soil conditions, suggests that the relation between the roots of *Calluna* and the micro-flora of the soil in which it is growing is an intimate one; that the balance between these biological factors may be very delicate, and only maintained in equilibrium, *i.e.*, in such relations that the result is either beneficial or indifferent to the plant, under definite soil conditions.

It is only by attacking this larger problem that a clue can be found to the soil conditions which determine growth in any given locality such as the one under consideration, where the soil differs in respect to certain constituents over a small area.

In the case of such plants as *Calluna* and its Ericaceous allies, the relation of the roots to the soil is evidently rendered more complex by the presence of a mycorhizal fungus, of which the full significance to the plant is still in need of demonstration. The details of fungal infection, and the ability of the plant to germinate and grow without its fungal partner have also yet to be described in the case of *Calluna*.

An obligate association of definite races of bacteria with the roots of plants has already been suggested[1], and it would seem not unreasonable to expect that such associations would become much more complex in the case of a plant, the roots of which constantly contain mycorhiza. It is claimed that several species of nitrogen-fixing fungi have been isolated and cultivated from the mycorhiza-bearing roots of various Ericaceous plants, including *Calluna vulgaris*, but absolute demonstration that this was the case could not be made, since the seedlings were never obtained in a sterile condition.[2] Similar relations are suggested far *Vaccinium corymbosum*,[3] and have indeed already been inferred for most plants which form root associations with either fungi or bacteria.

Before the main problem of the relations of the mycorhizal fungus to the plant and of the former to the soil and its bacterial flora can be attacked, it is necessary, therefore, to learn whether the association of the plant with its mycorhizal fungus is an obligate one, and for that purpose to determine the following points:—

(i). At what stage in the life-history of the plant, and from what source, does infection of the roots take place?

(ii). Is it possible (*a*) to germinate, (*b*) to grow *Calluna vulgaris* without infection of the roots under sterile conditions?

Having a knowledge of these facts, it should be possible to infer the existence, or not, of fundamental relations between the plant and special micro-organisms of the soil; to determine if any of the latter are indispensable for its growth, and whether the soil preferences and peculiarities of *Calluna* are directly associated

[1] Gottheil, O. "Botanische Beschreibung einiger Bodenbakterien." Centralbl. f. Bakteriologie, Bd. 7, p. 430.

[2] Ternetz, C. "Ueber die Assimilation des atmosphärischen Stickstoffes durch Pilze." Jahrb. f. wiss. Bot., Bd. 44, 1907, p. 353.

[3] Coville, F. V. "Experiments in Blueberry Culture." U.S. Dept. Agric. Bureau of Plant Industry, Bull. No. 193, 1911,

with them, or are specific to the plant, apart from its symbiotic relations with any other organism.

It has already been mentioned (page 64), that the roots of seedlings when germinated are always infected with mycorhizal fungus.

Microscopic examination of young seedlings, protected against infection from without during germination, shows that emergence of the radicle is accompanied by growth of fungal hyphæ from the testa. Some of these hyphæ grow across to the root and infect the seedling root, most commonly, *via* the cells of the root cap. This mode of infection appears to be very regular and characteristic. Bacteria are also associated with the seed-coat, but these are not conspicuous in seeds germinated under healthy conditions.

Infection of the seed-coat by fungi and bacteria occurs commonly in many seeds, such infection taking place after the seeds have been exposed to the air.[1] In the case of *Calluna* seeds, in addition to this superficial infection, a fungus is present, which is identical morphologically with the mycorhizal fungus present in healthy roots.

So far as could be ascertained from examination of fresh material, endosperm and embryo are free from infection in the resting seed. Microtome sectons of the seed pointed to infection of the testa only, and therefore to the possibility of sterilizing the seeds. The delayed infection observable in heated seeds (page 64) also supported this view, which has now been confirmed as correct, by germinating seedlings in a sterile condition, after adequate sterilization of the seed-coat.

It remains to enquire the source of infection and at what stage of seed development it takes place.

Examination of the ovary of the flower after fertilization reveals the fact that, in common with other parts of the flower the ovary wall is infected with fungal hyphæ.

Infection of the young seed-coat takes place from this source while the seeds are still enclosed in the ovary.

A full account of the details of this infection of the seed-coat, and of the mode of infection of the flower—whether from without at the period of flowering or from within by a more widespread distribution of the mycorhizal fungus in the plant than has been commonly assumed—is reserved for a subsequent paper.

Fungal infection of the testa is difficult to observe in the

[1] Arcichovskij, V. "Ueber die Methoden zur Gewinnung mikroorganismenfreier Samen." Centralb. f. Bakt., Bd. 36, 1912, Nos. 15—18.

resting seed, but in favourable cases the presence of hyphæ and more rarely of isolated spores can be demonstrated. The evidence at present available, points to infection of the coat by spores as relatively rare. This may, to some extent, account for the differential results obtained when attempting to sterilize seed. Effective sterilization is doubtless more difficult in the case of seeds, to which spores adhere so closely that they are not dislodged by washing or centrifuging. Attempts to sterilize the seed by immersion in hot water at 70°C., 60°C., and 52°C. respectively for fifteen minutes led to all the seeds being killed by the treatment. Seeds soaked in ·01% corrosive sublimate for five minutes always gave a large proportion of infected seeds when sown.

The following method was then tried and although sterile seedlings were not obtained, it yielded interesting results in another direction.

Soil extracts of the two soils were prepared, using 25 grams of fresh soil to 300 c.c. distilled water; agar, in the proportion of 1·5% was added and the media sterilized in the usual way.

Seed was sterilized by soaking for thirty minutes in ·01% corrosive sublimate, washed repeatedly with sterile water and sown with a sterile pipette in Petri dishes of the above media, which were kept for some days at a temperature of 37°C. At the end of five days the two sets of plates were strikingly different in appearance, this observation applying both to the sterilized cultures and to the controls for which unsterilized seed was used.

The results are summarized in Table II.

TABLE II.—SEED CULTURES IN AGAR SOIL EXTRACTS. TEMP. 37°C. 5 DAYS.

	SEED TREATED CORR. SUB. ·01%	CONTROL (SEED UNTREATED).
(A) "Heather" Soil Extract.	Many seeds apparently sterile. Some with a zone of mycelium. Plates sterile except in the immediate neighbourhood of seeds.	Majority of the seeds surrounded by a zone of mycelium. A few seeds apparently unaffected.
(B) "Chalk" Soil Extract.	Almost every seed or group of seeds with a zone of bacterial growth. Mycelium almost or entirely absent. Plates otherwise sterile.	Majority of seeds surrounded by bacterial colonies. Mycelium, if present, always accompanied by vigorous bacterial growth.

Since a majority of the seeds in each plate were infected, the Petri-dishes were opened and the growths examined microscopically. In the "chalk" soil cultures, well-defined bacterial colonies were present round all seeds but three, in a total of about one hundred seeds.

Hyphæ were absent from the outer limits of many of these colonies. In others mycelium was present but generally showed attenuated growth and the hyphæ were invested with a sheath of bacteria (Plate III, Fig. 6).

Masses of bacteria occurred in close association with the mycelium, which was rarely present in sufficient amount to alter the macroscopic appearance of the colony.

In the "heather" soil cultures a vigorous zone of mycelium was present around every infected seed. Mycelial growth round "sterilized" seeds was apparently pure but had not reached the sporing stage.[1]

Bacterial colonies, closely resembling those in the "chalk" soil cultures were present in many of the growths. These were not sufficiently prominent in any single case to affect the macroscopic appearance, which was always of a mycelial character.

The close association of bacteria with the hyphæ, which was a striking feature in the other plates, was not observable.

At this stage of development the difference in the two sets of plates was very striking:—

The cultures for which an extract of "heather" soil had been used were practically free from bacterial growth; in those for which an extract of the "chalk" soil was used they were the most prominent feature.

It was the striking contrast presented by this set of plates, in conjunction with the appearances noted in the roots of young seedlings growing in soil cultures, that first suggested the possibility of a biological relation between the mycorhizal fungus and soil bacteria.

It is significant that the mycelium grows v[illegible]sly in a medium made up with an extract of the one soil and is [illegible] of t[illegible]lly eliminated by bacterial growth in that made with an extract of the other soil, the seeds in both cases having had precisely similar treatment. The appearance of the hyphæ in the latter case strongly suggests that given certain conditions of nutrition, bacteria, constantly

[1] A fungus invariably present in these colonies has since then been identified with the species occurring as mycorhiza in the roots.

associated with the seed, can multiply and become pathogenic to the fungus which is also present on the seed coat. The same inference is suggested by the behaviour of the mycorhizal hyphæ on the roots in pot cultures of the "chalk" soil.

It is recognised, of course, that these pathogenic relations may be secondary in both cases, and determined by inability of the mycelium to thrive under the conditions supplied. In either case they seem to be pertinent to the inquiry. A large proportion of the seeds in these cultures germinated, and no difference was apparent either in rate of germination or in germination capacity. This difference of behaviour as compared with soil cultures may be due to the position of the seeds on the surface of the media, but requires further investigation. The seedlings grew for a month or more, but soon showed symptoms of starvation in all the cultures, due no doubt to the paucity of food material in the soil extracts.

The next attempt to sterilize seed was successful.

Similar extracts were prepared, made up with agar, sterilized, and placed in sterile Petri dishes. Seeds were soaked for thirty minutes in water, precautions being taken that the seed coats should be thoroughly wetted. They were then immersed for short periods (two minutes or less) in a 1% solution of corrosive sublimate, washed as before in many changes of sterile water and sown, fewer seeds being placed in any one dish. Care was taken to make the conditions as aseptic as possible and the cultures were placed under a bell-glass in a small greenhouse, all the surroundings having previously been washed down with a strong solution of Jeyes' fluid in water.

At the end of nineteen days three plates contained each a number of germinating seeds and were absolutely free from micro-organisms.

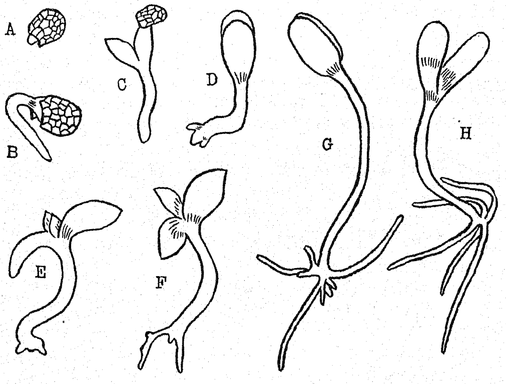
No trace of fungal or bacterial growth appeared round any of the seeds, about 50% of which germinated at the usual rate.

Early stages of growth of these sterile seedlings are otherwise normal and precisely similar to those of infected seedlings.

The seedlings were transferred singly to special culture tubes fifty-three days after sowing, *i.e.*, about five weeks after germination. Many of them formed several leaves and developed the rudiments of roots while still in the seed dishes (Text-fig. 1, A—F).

The cotyledons and young leaves were green and the seedlings appeared to be perfectly healthy, with the exception that they had made no attempt to send down roots into the culture medium, or

to place the axis in a vertical position. For comparison with these sterile seedlings, there are shown, in Text-fig. 1, two seedlings (G, H) germinated in moist air from unsterilized seeds and infected with mycorhiza.



Text-fig. 1. Seedlings of *Calluna vulgaris*. A to F, sterile seedlings germinated under aseptic conditions on agar plates. (A to C, four weeks after sowing; D to F, eight weeks after sowing). G and H, seedlings germinated in moist air, seeds unsterilized, seedlings infected with mycorhiza; eight weeks after sowing. All × 12.

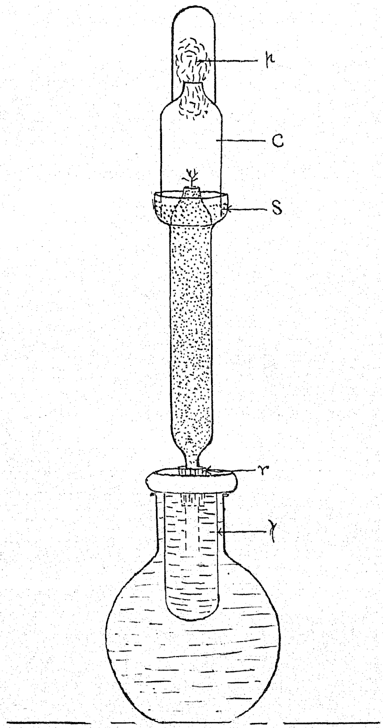
The tube shown in Text-fig. 2 is used for sand cultures; with slight modification similar tubes can be used, without filters, for water or agar cultures. After filling the sterilized tubes with agar media or with fine quartz sand as the case may be, the latter washed and sterilized in the usual way, the whole apparatus is sterilized again and when cool, is ready for planting.

After placing the filters in the solutions, the sand at the surface becomes moist, from capillary rise of the solutions, in about three hours.

The seedlings can be rapidly transferred to the tubes and the covers replaced. By filling the shoulder S with sterilized sand, the tubes can be manipulated without risk of knocking off the covers after sterilizing, and by moistening this sand with sterile water, a

moment before the joint is made air-tight with hot paraffin wax, the air inside the cover C is maintained in a moist condition.

Once planted and placed under suitable conditions, little attention is required.



Text-fig. 2. Apparatus for growing sterilized seedlings in sand cultures. Lettering :—*p*, cotton wool plug ; *c*, glass cover ; *s*, shoulder filled with sterile sand ; *r*, rubber cork ; *f*. Massen filter candle.

The evidence available as a result of these cultures points to the conclusion that roots are not formed by the seedlings unless infection with a fungus associated with the seed-coat takes place: and that therefore the relations between the plant and its endotrophic fungal partner is an obligate one, under the conditions supplied, *viz.*, a supply of inorganic salts, in a solution favourable to the healthy growth of unsterilized seedlings.

Since roots are not formed, it is impossible to demonstrate with certainty how far the susceptibility of the roots to particular salts and to the concentration and the reaction of the culture media are specific characters of the plant.

It is proposed to deal more fully with these and similar cultures and with the effects of inoculation from a pure culture of the fungus in a subsequent paper.

The evidence is conclusive that the resting embryo of *Calluna* is uninfected; also that, by effective sterilization of the seed-coat, seedlings can be germinated in a sterile condition and can be maintained alive under aseptic conditions for six months or longer. Infection of the plant by the fungus takes place under normal conditions immediately after germination and it is believed that a functional root-system is not formed by the seedling unless such infection occurs.

Hence, the nutrition of *Calluna* is bound up with that of its mycorhizal fungus: and the soil preferences of the plant and the soil conditions which limit its growth are determined *indirectly*, by the ability of the fungus to flourish under the conditions supplied.

In short, the maintenance of a definite biologic relation between the roots and the fungus which infects them acts as a limiting factor to the spread of the plant.

The refusal of *Calluna* to grow in the calcareous soil investigated, and presumably in similar soils elsewhere, is due to a disturbance of these conditions. On this view, the habit usually described as "calcifuge" may be, in this case, characteristic of the fungus rather than of the plant.

Directly connected with this disturbance is the presence of colonies of bacteria closely associated with the roots, especially with the regions where the fungus is usually prominent.

It is suggested that the bacteria are to be regarded either as pathogenic agents, or as indicators of soil conditions unfavourable to the fungus and therefore ultimately to the plant.

There is no doubt that the abnormal growth exhibited by the roots in unfavourable soil is directly correlated with the presence of an investing sheath of bacteria on these roots, but the evidence is not conclusive that the organism concerned is the inducing cause of the unhealthy condition.

SUMMARY.

1. As shown in a previous communication, small and sharply defined communities of *Calluna vulgaris* occur on the Wiltshire and Berkshire Downs, associated with soils on clay-with-flints.

The distribution of these heather communities is anomalous, in that they have monopolized areas of fertile soil.

Experimental work was undertaken to investigate the nature of the factors which limit the spread of *Calluna* from these areas to the surrounding down soils and indirectly to throw light on the significance of the calcifuge habit as shown by the soil relations of *Calluna* and its allies.

2. As demonstrated by pot cultures in soil from (*a*) a heather area, (*b*) soil overlying chalk, *Calluna vulgaris* grows *normally* in the former, *abnormally* in the latter.

3. Abnormality of growth is exhibited in (*a*) reduced germination capacity, (*b*) retarded germination, (*c*) arrest of root and curvatures of growing region, (*d*) arrest of shoot, (*e*) small size and red colouration of leaves.

4. Intimately connected with these abnormalities is the presence of colonies of bacteria on the roots, especially around the tip, and also a marked diminution of vigour in the growth of the mycorhizal fungus.

5. The abnormalities of growth can be *induced* in seedlings growing in "heather" soil by watering with filtered extracts of the unfavourable soil, if the treatment is continued over a considerable period. The unfavourable factors are presumably of a chemical nature.

6. The result of germinating unsterilized or imperfectly sterilized seeds in agar media, made up with extracts of the two soils named, shows that the development of the fungal and bacterial elements of the micro-flora associated with the seed-coat is determined *qualitatively* by the nature of the soil extract used.

With an extract of the heather soil, the mycelial constituent is predominant; with an extract of the down soil, colonies of bacteria

constitute the prominent feature of the growths associated with the seed-coat.

7. Seedlings of *Calluna vulgaris* are infected by the mycorhizal fungus immediately after germination.

Infection of the primary root takes place by a growth of mycelium from the seed-coat, the latter being infected while still in ovary.

8. The resting embryo and endosperm are free from infection.

9. The fungus isolated from the seed-coat is morphologically identical with one obtained in agar cultures of pieces of healthy root.

10. Seeds can be sterilized and seedlings germinated in a sterile condition, *i.e.*, free from fungal or bacterial infection.

The germination and *early* stages of growth of such sterile seedlings are normal, but in the absence of infection complete arrest of root-formation occurs.

11. The evidence at present available points to the conclusion that the relation between *Calluna* and its mycorhizal fungus is an obligate one, and that successful growth of the plant is ultimately bound up with infection of the roots at an early stage by the fungus, and with the subsequent healthy growth of the latter; hence, the soil preferences exhibited by the plant depend on the maintenance of a biological balance between the roots and the constituents of the microflora which beset them.

12. On this view, the inability of *Calluna* to flourish in the soil investigated is due to a disturbance of the relations maintained under favourable soil conditions between the roots of the plant and its mycorhizal fungus.

The bacterial colonies associated with the roots, more especially with the regions where the fungus is usually prominent, are to be regarded either as pathogenic agents, or as indicators of soil conditions unfavourable to the fungus. The evidence available points to the bacterial colonies as directly correlated with the abnormal growth displayed by the roots, but is not at present *conclusive* that they are the immediate cause of that condition.

13. Water cultures of *Calluna* have not up to the present thrown any light on the significance or not of the relatively high ratio of MgO to CaO in the soil in the area investigated.

They confirm previous observations as to the inability of the plant to thrive in any but very weak solutions.

DESCRIPTION OF THE PHOTOGRAPHS ON PLATE III, ILLUSTRATING MISS RAYNER'S PAPER ON "THE ECOLOGY OF *CALLUNA VULGARIS*."

Fig. 1a. *Calluna* seedlings from "heather" soil, showing normal root and shoot development; six months old.

Fig. 1b. *Calluna* seedlings from "heather" soil treated with carbon bisulphide vapour; six months old. The more vigorous growth as compared with Fig. 1a is less marked than at an earlier stage.

Fig. 1c. *Calluna* seedlings from "chalk" soil, showing arrest of root and shoot development; six months old.

Fig. 1d. *Calluna* seedlings from "chalk" soil treated with carbon bisulphide vapour; six months old. As compared with Fig 1c, root development is more normal.

Fig. 2a. Apex of a young *Calluna* root from "heather" soil, showing normal conditions.

Fig. 2b. Apex of *Calluna* root of same age from "chalk" soil, showing abnormal condition with bacterial investment.

Fig. 3. Part of root apex shown in Fig. 2b, more highly magnified, to show bacteria in sheath.

Fig. 4a. *Calluna* seedling in "heather" soil watered for six months with an extract of "chalk" soil.

Fig. 4b. Control—similar seedling watered during the same period with distilled water.

Fig. 5. *Calluna* seedling from "chalk" soil, watered for six months with an extract of "heather" soil. Control seedlings in similar soil watered with distilled water all died before the end of the experiment. Fig. 1c shows surviving seedlings of the same age in this soil from another series of experiments.

Fig. 6. Mycelium from fungal colonies surrounding seeds, in agar cultures of "chalk" soil, to show investing sheath of bacteria.

RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

By F. Cavers.

(Continued from p. 36).

IV.—Relation of Green Algæ to Chlamydomonads.

THERE appears to be strong support for the view that the majority of the Green Algæ may be derived from Flagellate ancestors with two or more equal flagella. In 1897, Chodat (24) pointed out that in the life-history of the lower Green Algæ there may be distinguished three conditions, either of which may become dominant, the other two being then transient or suppressed: (i.) the zoospore condition or motile stage; (ii.) the sporangium condition or unicellular motionless stage; (iii.) the palmelloid condition, in which non-motile cells are connected into aggregates by cell-walls at right angles to each other. In 1900, Blackman (6) published an important paper on the phylogeny of the Algæ, containing not merely a critical summary of modern work bearing upon the problem, but also various far-reaching suggestions as to the lines along which the evolution of the different Algal groups may be traced from Flagellata. Blackman pointed out that among the simple Green Algæ which constitute the group of Protococcoideæ three divergent vegetative tendencies are observed: (i.) a Volvocine tendency towards the aggregation of motile vegetative cells into gradually larger and more specialised motile cœnobia; (ii.) a Tetrasporine tendency towards the formation of aggregations by the juxtaposition of the products of septate vegetative cell-division to form non-motile organisms of increasing definiteness and solidarity; (iii.) an Endosphærine tendency towards the reduction of vegetative division and septate cell-formation to a minimum. The simplest forms showing any one of these tendencies seem clearly to diverge from species of the genus *Chlamydomonas*, which may be regarded as the phylogenetic starting-point of the various lines of Green Algal descent. The line arising from the Volvocine tendency leads to the Volvocales and culminates in *Volvox;* the outcome of the Endosphærine tendency is seen in the Siphoneæ; while the Tetrasporine line has given rise to the great majority of the Green Algæ and through these to the Archegoniatæ and other higher plants.

The phylogeny of the Conjugatæ, Œdogoniales, and a few other isolated groups of filamentous Green Algæ remains in some doubt, owing to the absence of undoubted transitional forms connecting these groups with either the Tetrasporine line on one hand or with distinct Flagellate ancestors on the other. For further details regarding the phylogeny of the Green Algæ, reference should be made to the paper by Blackman already mentioned (6), and to the

classification based by Blackman and Tansley (7) upon the principles set forth in that paper; also to the systematic works on Algæ by Oltmanns (95), West (146), and Lotsy (89), in which due prominence is given to modern views of Algal phylogeny. More recently, Fritsch (46) has published a valuable paper, in which is included a useful bibliography; while Pavillard (114) has contributed a resumé of some modern work on Vegetable Protistology—though his "revue rapide" omits entirely the Brown Flagellata and lower Brown Algæ, on which some remarkably interesting work has been published during the last few years.

The relationships of the three lines of Flagellate-Algal descent here suggested are indicated in the accompanying Table A, a fuller explanation of which will be given later.

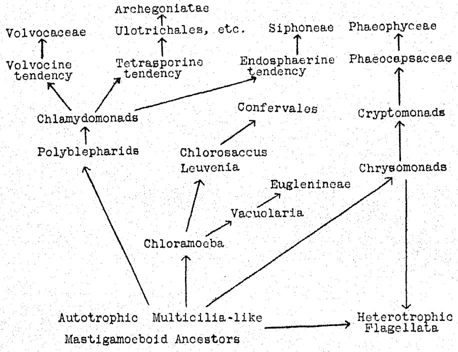


Table A.—Suggested Phylogeny of (I) the Polyblepharid and Chlamydomonad, (II) the Chloromonad, and (III) the Chrysomonad and Cryptomonad lines. For details see text.

Since 1900, perhaps the greatest advances in the study of those Flagellates which are more obviously important in connexion with the phylogeny of the Algæ have been made among the Chrysomonads and Cryptomonads, but before dealing with these we may consider some interesting additions to our knowledge of the group of Green Algæ whose evolution from the Flagellata has, on the whole, been most completely worked out—namely, the Volvocales, using this name to include the entire series of organisms (the "Phytoflagellata" of various zoological writers) representing the transition from Flagellate ancestors to the motile unicellular Green Algæ (Chlamydomonads) and the outcome of the Volvocine tendency which leads to the formation of increasingly complex motile cœnobia and culminates in *Volvox*.

V.—Volvocales.

The Polyblepharidaceæ are included in the Volvocales by Blackman and Tansley (7), Wille (150), and various other writers, though Fritsch (46) regards them as still belonging to the Flagellata, but it appears quite immaterial how this family is placed in a formal scheme of classification, so long as it is recognised that no sharp line of division separates the Flagellata from the lower Algæ and that this remarkable transitional family shows an extraordinarily even balance between the two groups. The Polyblepharids agree with typical Flagellates in being devoid of a definite cellulose wall and in undergoing longitudinal division in the motile phase—but it should be noted that in several genera of Volvocales (*Chlorogonium*, *Brachiomonas*, and even colonial genera like *Gonium* and the oogamous *Eudorina*) division may occur while the flagella are still motile. The Polyblepharids have the characteristic basin-shaped Volvocine chromatophore and a pyrenoid, but—as will appear later—the Cryptomonads and some of the other Chrysomonadineæ would have as much right to a position among the Algæ as have the Polyblepharids if the possession of Algal chromatophores, pyrenoids, starch, and a firm periplast allowing of only slight changes of shape be taken as definitely Algal characters; while, on the other hand, the fact that sexual reproduction occurs in a Polyblepharid *(Dunaliella)* cannot now be regarded as an argument against the reference of this family to Flagellata rather than to Algæ.

Probably the most primitive genus of Polyblepharidaceæ is *Polyblepharis* (Fig. 2, A), in which the broader anterior end of the conical body bears from six to eight flagella in a tuft; in *Pyramimonas* (Griffiths, 52; Fig. 2, B, C) there are four flagella arising from a depression at this end, which is four-lobed, as is also the chromatophore; in *Chloraster* (Fig. 2, D) there is a central fifth flagellum; while in *Tetratoma*, a somewhat doubtful and incompletely known form, there are four flagella inserted at separate points on the anterior half of the spherical body. The genus *Dunaliella* (Fig. 2, E to L), recently described by Hamburger (53) and by Teodoresco (140, 141), evidently forms a transition from the Polyblepharidaceæ to the Chlamydomonads, since it has only two flagella and shows conjugation of isogamous zoogametes; while *Stephanoptera*, recently discovered by Dangeard (35), resembles *Pyramimonas* in structure but has only two flagella, thus connecting *Pyramimonas* with *Dunaliella*—according to Dangeard, the life-cycle of *Stephanoptera* ends in encystment, the cyst having sometimes two nuclei instead of one, but the fate of the cyst was not determined. To the Polyblepharidaceæ probably also belongs the genus *Chlorodendron* (Fig. 2, M to B), placed by Oltmanns (95) in a special family (Chlorodendraceæ), with the closely related, or perhaps congeneric, forms *Prasinocladus lubricus* Kuckuck and *Euglenopsis subsalsa* Davis—these have recently been investigated by Dangeard (34, 36) who regards these forms as being closely related to the Carteriaceæ (see below). In the Chlorodendreæ, branching colonies are produced by the localised secretion of mucilage derived from the periplast, or cell-wall, of the dividing cells, and this family, or sub-family, forms

an interesting side-line of colonial development arising from a *Pyramimonas*-like type.

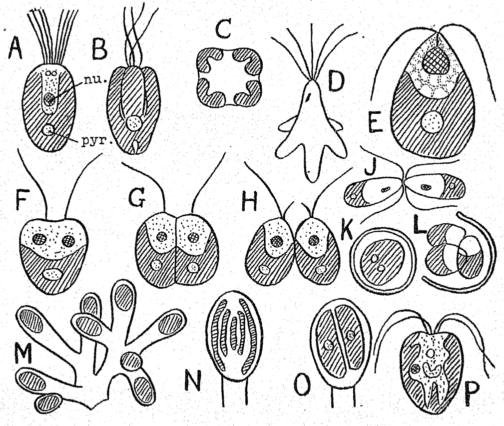


Fig. 2. POLYBLEPHARIDACEÆ.—A, *Polyblepharis singularis* Dang. B, C, *Pyramimonas delicatulus* Griffiths: C, anterior view showing extremities of lobes of chromatophore. D, *Chloraster gyrans* Ehrb., showing stigma or "eye spot." E to L, *Dunaliella salina* (Dun.) Teodor.: E, vegetative cell, with bell-shaped chromatophore, large nucleus, and reticulate protoplasm; F, G, H, stages in division; J, conjugation of zoogametes; K, zygospore; L, rupture of zygospore to set free the zoospores. M to P, *Chlorodendron lubricum* (Kuck.) Senn: M, a portion of a colony; N, a single cell of same; O, division of cell; P, motile cell or zoogonidium. A from Dangeard; B, C, from Griffiths; D, from Stein; E and J, from Hamburger; F, G, H, K, L, from Teodoresco; M to P, from Kuckuck.

In setting forth a new classification of the Volvocales, Pascher (108) has adopted the suggestions made by Oltmanns as to the affinities between *Carteria* and *Spondylomorum*, and by Schmidle as to those between *Sphærella* and *Stephanosphæra*, and has separated these genera from the remaining Volvocales, dividing this order into the four families, Polyblepharidaceæ, Carteriaceæ, Sphærellaceæ, and Chlamydomonadaceæ. Wollenweber (153) has suggested that the Volvocine line shows progressive reduction in the number of flagella and of contractile vacuoles, hence *Carteria* and *Sphærella* may be regarded as more primitive than the Chlamydomonads, the former in having four flagella and the latter in having numerous contractile vacuoles (as many as sixty in *S. Drœbakensis*). It is, however, rather difficult to determine just which cytological characters should be regarded as relatively primitive and which as relatively advanced among the Volvocales. For instance, numerous

contractile vacuoles are found not only in *Sphærella* but also in *Chlorogonium* (which differs from the Polyblepharids and most of the simpler Chlamydomonads in showing transverse instead of longitudinal division), and in *Agloë*, a form with somewhat specialized cell structure. *Carteria* and *Spondylomorum* agree in having four flagella and in other characters, but though *Carteria* is usually stated to have a pyrenoid, Jacobsen (61) has described a species (*C. ovata*) which has none; according to this writer, *Spondylomorum* is also without a pyrenoid; while *Chloromonas* is distinguished from its ally *Chlamydomonas* solely on the ground that it lacks a pyrenoid, but this simply means that systematists have described pyrenoidless species or even varieties (Serbinow, 137) of *Chlamydomonas* as belonging to a distinct genus—on other grounds, there is little doubt that *Chlamydomonas* and *Chloromonas* are quite unnatural genera, and will probably have to be revised and split up as the result of further investigations. Most of the Volvocales have a single pyrenoid, but in *Chlamydomonas inhærens* (Bachmann, 3) two or three of these bodies may be present, while in *C. coccifera* (Goroschankin, 51, iii) there are five to eight pyrenoids; two occur in *Sphærella Drœbakensis* and in *Stephanosphæra*, while *Sphærella pluvialis*, *Chlorogonium*, and *Pleodorina* have a large number of pyrenoids.

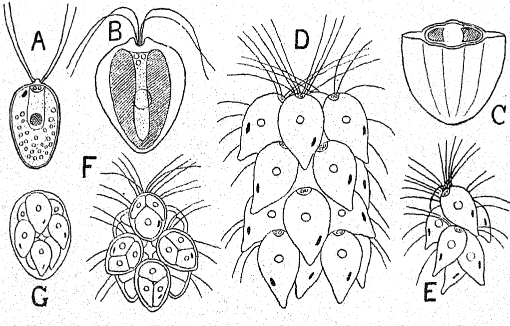


Fig. 3. CARTERIACEÆ.—A, *Carteria ovata* Jacobsen: this species has no pyrenoid, the chromatophore contains numerous small starch grains. B, C, *Scherffelia phacus* Pascher: C shows the cell cut across, to make clearer the wing-like expansion of the cell-wall and the structure of the U-shaped chromatophore. D to G, *Spondylomorum quaternarium* Ehrb.: D, a normal sixteen-celled cœnobium; E, an eight-celled cœnobium; F, division of each cell to form a daughter cœnobium; G, daughter cœnobium not yet set free from mother-cell. A, D to G, from Jacobsen; B, C, from Pascher.

The family Carteriaceæ includes *Carteria* (Fig. 3, A), which has a very thin wall; *Scherffelia* (Fig. 3, B, C), in which the cell is flattened, oval in outline and slightly biconvex in cross-section,

with a thick wall which in one species is produced into a marginal wing on either side, two chloroplasts which may or may not be united behind to form a U-shaped structure (obviously derived from splitting of an originally basin-shaped chromatophore), and no pyrenoid; *Tetrablepharis*, a colourless saprophytic form probably derived from *Carteria*; and *Spondylomorum* (Fig. 3, D to G), a colonial form constructed on a plan quite different from that seen in the cœnobial Chlamydomonadaceæ and consisting of sixteen *Carteria*-like cells in four alternating tiers of four cells each, attached to a gelatinous rod-like axis. Among the Carteriaceæ, sexual reproduction is only known in one or two species of *Carteria* which produce isogamous zoogametes. It is of interest to note that the symbiotic "Zoochlorella" found in the Planarian worm *Convoluta roscoffensis* (Keeble and Gamble, 65) is a species of *Carteria*; the single species of *Spondylomorum* (*S. quaternarium*), hitherto known only from Europe and Asia, has recently been discovered by Campbell (20) in California.

Apart from the Polyblepharidaceæ and Carteriaceæ, the Volvocales have a pair of flagella, though a single flagellum occurs in a species of *Polytoma* (Pascher, 108) and in the genus *Mastigosphæra*. The Sphærellaceæ, including the unicellular *Sphærella* (*Hæmatococcus*) and the colonial *Stephanosphæra*, are distinguished from the remaining Volvocales—the Chlamydomonadaceæ—mainly by the peculiar structure of the cell-wall. Various contributions to the knowledge of *Sphærella* have recently been made, especially by Peebles (110), Reichenow (113), and Wollenweber (145, 146). What has usually been taken for a thin outstanding cell-wall is in reality a firm outer layer, while the supposed sap-containing space between wall and protoplast is a thick inner gelatinous coat, traversed by fine branching pits into which protoplasmic threads extend. Reichenow has minutely studied the structure and mitotic division of the nucleus and the shifting of the originally longitudinal axis of division into an oblique or transverse position. The chloroplast is a spongy and reticulate structure, and in *S. pluvialis* there are numerous pyrenoids at the nodes of the network. Though *Sphærella* has been so much worked at, Miss Peebles appears to have been the first to observe a sexual process in this genus; she states that when dry encysted cells of *S. pluvialis* are moistened and exposed to strong light, the contents of the cyst divide into eight to sixty-four gametes which fuse in pairs, as is also the case in *Stephanosphæra*.

(*To be continued*).

[NOTE.—In the first instalment of this article (January number), certain alterations inserted at the last moment resulted in misprints. On p. 28, "former" (line 7) should, of course, be "formal"; on p. 32, line 3 from bottom, for "form" read "forms"; on p. 33, top line, for "Crystoflagellata" read "Cystoflagellata," and in line 5 from top "hetetrotrophic" should be "heterotrophic." On p. 33, line 18 from top, the substitution of a note of interrogation (?) for a semicolon (;) may be regarded as a piece of unconscious humour—though the reader may, like the author, feel inclined to mark *each* of these "main lines" with a query!]

REVIEW,

"Herbals: their Origin and Evolution. A Chapter in the History of Botany, 1470—1670." By Dr. Agnes Arber. Cambridge Univ. Press, 1912.

No other epoch in the development of Botany has the peculiar fascination possessed by that which elapsed between the renascence of interest in the subject and its firm establishment as a pure science. Botanists are extremely fortunate in having in Dr. Arber a writer who combines a thorough knowledge of the recent growth of the science with an affectionate interest in its childhood and an unrivalled acquaintance with its juvenilia. To these qualifications she adds the other not less important one of literary ability, so, that in a book positively loaded with erudition there is no indigestible page: indeed no page in which one may not find some some happy phrase or quaint quotation.

The book opens with a consideration of the earliest known records of observations of plants, those of Aristotle, Theophrastus, the elder Pliny, Dioscorides and Albertus Magnus, although these authors lived earlier than the XV century: their work, especially that of Dioscorides, having such a fundamental importance in relation to the mediæval botany of the Renaissance. The primitive Herbals of the end of the XV century, with their crude, but singularly attractive illustrations, are next considered. A special chapter is devoted to the earliest examples of herbals in England; and here, as in the other sections dealing with works in English, Dr. Arber exhibits to the full her aptitude in the selection of charming passages for quotation.

The next chapter is the most extensive in the book, and deals with the history of the herbal in Germany, the low Countries, Italy, Switzerland, France and England respectively. This is probably the best arrangement of the mass of available material: but it is remarkable to note the internationalism of botanical studies even in those early days. Here we find ourselves among Bock and Brunfels, Fuchs and Camerarius, and witness the culmination of the art of plant portraiture.

Chapter V is devoted to the methods adopted in plant description, and Chapter VII to the evolution of botanical illustration. The latter is admirably full, dealing concisely with the characteristics of the work of the various artists and the development of the power of scientific observation reflected therein: the text being lavishly adorned with well chosen figures reproduced through the skill of Mr. W. Tams.

Of great interest to systematists is Chapter VI on early methods of classification: while the curious will find in Chapter VIII an account of the singular entanglement of botany with astrology; and of the doctrine of signatures, the climax of the anthropocentric notions which have so recently disappeared from orthodox science.

The volume closes with a list of herbals published between 1470 and 1760, a bibliography and a full iudex. It well printed and bound, and singularly free from misprints. By reason of its varied virtues it will appeal to a wide circle of readers, and will keep alive many valuable things upon which in the lapse of time "oblivion blindly scattereth her poppy." R.H.C.

THE

NEW PHYTOLOGIST.

VOL. XII, No. 3. MARCH, 1913.

[PUBLISHED APRIL 15TH, 1913].

A BRITISH FOSSIL *SELAGINELLA*.

BY A. C. SEWARD, F.R.S.

[WITH PLATE IV].

THE fact that the genus *Selaginella* is now represented by a single species in the British Flora adds interest to the discovery of a Wealden species differing in habit from the recent type. Palæobotanical literature contains numerous records of herbaceous Lycopods, referred to *Lycopodites*, *Selaginites*, *Lycopodium*, or *Selaginella*, but it is only in a very few cases that the untrustworthy eivdence supplied by a superficial resemblance of the impressions in habit and leaf-form to recent species is confirmed by the discovery of spores.[1] It is almost impossible in many cases to distinguish fossil vegetative shoots of lycopodiaceous plants from those of certain Conifers and Bryophytes or even from some types of Dicotyledons, In the absence of sporangia or spores or of clear evidence of dimorphic foliage the identification of small fossil impressions as species of *Lycopodites* or *Selaginites* seldom rests on a satisfactory basis.

The old generic name *Selaginites* has frequently been applied to fossils which afford no evidence of a closer relationship to *Selaginella* than to *Lycopodium*. In order to avoid the danger of a *suggestio falsi* associated with the use of a name clearly implying affinity to the recent genus, Zeiller[2] instituted the designation *Selaginellites* for fossil herbaceous lycopods which possess two kinds of spores, Brongniart's genus *Lycopodites* being conveniently retained for isosporous types or for such sterile specimens as may with reasonable certainty be regarded as generically identified either with *Lycopodium* or *Selaginella*. Although the great majority of existing Selaginellas differ from *Lycopodium* in the possession of two sizes of foliage leaves, there are some members of the former genus, e.g., the British species *S. spinosa*, which bear leaves of one type only.

[1] For a general account of fossil herbaceous lycopods, see Seward (10), pp. 78-91.

[2] Zeiller (06), p. 140.

Selaginellites Dawsoni sp. nov. Plate IV. 1894. Planta incertæ sedis, Seward, Wealden Flora, Pt. I, p. 20, Pl. I, figs. 8, 9.

The specimens on which this species is founded were obtained by the late Mr. Rufford of Hastings from the Fairlight Clay, at the base of the Wealden series at Ecclesbourne on the Sussex coast. I have called this Wealden species *Selaginellites Dawsoni* after Mr. Charles Dawson of Lewes, to whose enthusiasm and generosity the British Museum is indebted for many specimens of plants from the Sussex coast.

In the first volume of the Catalogue of Wealden plants in the British Museum a small branched shoot, agreeing closely with that shown in Fig. 1, was described under the non-committal title "Planta incertæ sedis" but, at the suggestion of Mr. Carruthers, it was compared with the slender spore-bearing branches of species of *Lycopodium* included in the *L. Phlegmaria* section.[1] Attention was also called to its resemblance to Conifer shoots of the type frequently referred, without any satisfactory evidence, to such genera as *Widdringtonites* or *Glyptostrobus*.

While recently engaged in the description of Wealden plants[2] acquired by the British Museum since the publication of the second volume of the Wealden Catalogue, I found the specimens represented in Figs. 1 and 2, both preserved on one piece of ironstone from Ecclesbourne but not actually in contact. The smaller fossil shown in Fig. 2 consists of portions of two axes approximately 2 mm. broad, with indistinct impressions at the edges of small crowded leaves and bearing several spherical sporangia 0.3 mm. in diameter on the surface (Fig. 2a). On treatment with nitric acid and potassium chlorate, a method recently described by Mr. Thomas in this Journal,[3] the sporangial walls were dissolved without revealing any microscopical features but numerous microspores and a few megaspores were obtained (Figs. 3 to 7). The microspores tended to adhere together in masses (Fig. 5) and not infrequently in compact tetrads (Fig. 3), the fourth spore in each tetrad being clearly distinguished on focussing. The microspores are approximately 0.04 mm. in diameter and are characterised by a finely tuberculate

[1] Seward (94), p. 20, Pl. i, figs. 8, 9. (Rufford Coll., British Museum, No. V. 2328). The specimen reproduced on Plate IV, also from the Rufford Collection, is No. V. 3151.

[2] A short account of *Selaginellites Dawsoni*, without illustrations, is included in the account of these recently acquired Wealden plants communicated to the Geological Society of London.

[3] Thomas ('12).

or pebbled[1] outer coat which gives them a pitted appearance, the depressions between the short rounded tubercles giving the impression of small circular pits (Figs. 4, 5). The three-rayed marking is very distinct on the wall of the spore reproduced in Fig. 4. The megaspores, 0.30-0.35 mm. in diameter, are usually oval or almost spherical with a three-sided pyramidal apex. As seen in Fig. 6, which represents the greater part of one spore with a portion of a second in close association, the thick wall has an irregularly reticulate surface precisely as in the megaspores of several recent species.[2] Fig. 7 illustrates the difference in size between the two kinds of spore and shows the wall of the megaspore opening along the three-rayed apical ridge. In the interior of one of the megaspores a thin inner membrane was noticed, separated a short distance from the much thicker outer wall, presenting an appearance very similar to that in recent megaspores where the exine and intine are often widely separated.[3]

The very close resemblance, which it may fairly be said amounts to identity, between the basal narrower portion of the fertile fragment shown in Fig. 2 and the vegetative shoot reproduced in Fig. 1 leaves no doubt as to the connexion between these two closely associated specimens. The sterile tufted shoot (Fig. 1), which is undoubtedly specifically identical with that reproduced in the Wealden Catalogue, shows on slight magnification the impressions of small broadly triangular leaves, the tips of which are indicated at the edges of the enlarged portion shown in Fig. 1a. The preservation does not admit of any definite statement as to the occurrence of one or two forms of foliage-leaves.

While it is clearly impossible to speak with confidence as to the precise relationship of the Wealden plant to existing species, there are certain recent types to which it exhibits a very close resemblance, particularly *Selaginella rupestris* Spring. In its densely tufted habit, small leaves, and slender branches this "most widely-spread species of the genus",[4] which does not occur in Europe, is strictly similar to the fossil form. The agreement presented by the vegetative shoot extends to the spores: the microspores, 0.45 mm. in diameter, have a finely reticulate or pitted exine, and the megaspores, 0.4 mm. in diameter, are characterised by the same

[1] Lyon ('01): the expressive term pebbled is used in describing the exine of the microspores of *Selaginella apus*, which agree closely with those of *Selaginellites Dawsoni*.

[2] For good figures of recent spores, see Hieronymus ('02). Some megaspores of species of *Selaginella* are figured also by Bennie and Kidston (88), Pl. vi, figs. 22-24.

[3] Fitting ('00), Pl. vi, fig. 23; Heinsen (94), Pl. xvi, figs. 5-7.

[4] Baker ('87), p. 35.

kind of reticulate sculpturing as is faintly shown in Fig. 6. Amongst other recent species of similar habit are *S. borealis* Spring, from East Siberia, the Eastern Himalayas, and other regions; *S. involvens* Spring, a Far Eastern type; and *S. cuspidata* Link from Mexico, Cuba, and Central America.

The spores of several recent species are almost identical both in size and surface-features with those of the fossil: the microspores of *S. serpens* and *S. canaliculata* are respectively 0.03 and 0.04 mm. in diameter; the reticulate spores of *S. Martensii* are 0.03 mm. (microspores) and 0.35-0.40 mm. (megaspores) in diameter. In some recent species the spores are larger: in *S. emiliana* the microspores have a diameter of 0.07 mm., while the megaspores exceed 1 mm.

In the Upper Carboniferous species *Selaginellites primævus* (Gold.) and *S. elongatus* (Gold.)[1] the megaspores, the only spores so far discovered, are respectively 0.4-0.5 mm. and 0.45 mm. in diameter. In *S. Suessii* Zeill. the megaspores are 0.50-0.65 mm. in diameter and are provided with an equatorial flange like that on the spores of *Selaginella caulescens*, while the microspores have a diameter of 0.04-0.06 mm. In this French species from the Coal-measures (Stephanien) of Blanzy there are 16-24 megaspores in the megasporangia.[2] In *Selaginellites Dawsoni* the number has not been determined.

Several Cretaceous and Jurassic species of *Lycopodites* have been described from British and foreign localities, but without information as to the nature of the spores it is impossible to assign them to a definite position in the Lycopodiales.

[1] Halle ('07), p. 9.

[2] Zeiller ('06), p. 141, Pls. xxxix-xli.

REFERENCES.

Baker, J. T. ('87). "Handbook of the Fern Allies." London.

Bennie, J., & R. Kidston. ('88). "On the occurrence of Spores in the Carboniferous Formation of Scotland." Proc. R. Phys. Soc. Edinburgh, Vol. IX, 1885-88.

Fitting, H. ('00). "Bau und Entwickelungsgeschichte der Makrosporen von *Isoëtes* und *Selaginella* und ihre Bedeutung für die Kenntniss des Wachsthums pflanzlicher Zellmembranen." Bot. Zeit., Bd. LVIII, p. 107.

Halle, T. G. ('07). "Einige Krautartige Lycopodiaceen Paläozoischen und Mesozoischen Alters." Archiv. Bot. (Stockholm), Bd. VIII, No. 5.

Heinsen, E. ('94). "Die Makrosporen und das Weibliche Prothallium von *Selaginella*." Flora, Bd. LXXVIII, p. 466.

Hieronymus, G. ('02). In "Die Natürlichen Pflanzenfamilien." (Engler and Prantl). Teil. I, Abt. iv., p. 621. Leipzig.

Kidston, R. See Bennie and Kidston.

Lyon, F. M. ('01). "A Study of the Sporangia and Gametophytes of *Selaginella apus* and *S. rupestris*." Bot. Gaz., Vol. XXXII, p. 124.

Seward, A. C. ('94). "Catalogue of the Mesozoic Plants in the Department of Geology, British Museum. The Wealden Flora, Pt. I." London.

,, ('10). "Fossil Plants." Vol. II. Cambridge.

Thomas, H. Hamshaw ('12). "On some methods in Palæobotany." New Phytologist, Vol. XI. No. 4, p. 109.

Zeiller, R. ('06). "Bassin houiller et Permien de Blanzy et de Creusot." Paris.

EXPLANATION OF PLATE IV.
ILLUSTRATING PROFESSOR SEWARD'S PAPER ON "A BRITISH FOSSIL *SELAGINELLA*."

Selaginellites Dawsoni sp. nov. (The author is indebted to Mr. Hamshaw Thomas for the photograph reproduced in Fig. 7. Figs. 1-2 were drawn by Mr. Brock and Figs. 3-6 are from photographs by Mr. Tams).

Figs. 1, 1a. Sterile Shoot. Fig. 1. Nat. Size; Fig. 1a, × 3.

Figs. 2, 2a. Fertile Shoot. Fig. 2. Nat. Size; Fig. 2a, × 3.

Figs. 3, 4, 5. Microspores. Figs. 3, 4, × 300; Fig. 5, × 100.

Fig. 6. Megaspore, × 100.

Fig. 7. Megaspore and microspores, × 100.

THE EVOLUTION OF THE HIGHER UREDINEÆ.

By W. B. Grove, M.A.

[With Two Figures in the Text].

ONE of the most pregnant phenomena attending the study of the Uredineæ during the present century has been the discovery by Tranzschel of the heterœcism of *Puccinia Pruni-spinosæ*, the Plum Rust. He proved what was previously not even suspected, that it has its æcidial stage on *Anemone coronaria*. But it is not the *fact* of the discovery, but the *method* which led up to it, that is of the greatest importance. This method has already led to several important results and will undoubtedly lead to numerous discoveries in the future, but its present advantage is that it gives us a view of the evolution of the Uredineæ which is based upon certain facts, and not upon uncertain speculations.

The facts are these:—In Europe and North America *Anemone nemorosa* bears a Micropuccinia, known as *Puccinia fusca* Winter, which has teleutospores of a very uncommon character (Fig. 1, A), —they have the two cells for the most part globular (especially the upper one), divided therefore by a deep constriction, easily separating from one another, covered all over with rather large coarse warts, and attached in bunches of 10—20 by short pedicels to

a common base. The teleutospores are accompanied by spermatia, but by no other spore forms. Now the teleutospores of *P. Pruni-spinosæ* (Fig. 1, B) on *Prunus* are absolutely identical with these, although they are accompanied (contrary to those of *P. fusca*) by uredospores and not by spermogones. These uredospores (Fig. 1, C) are also of a very uncommon shape; they have the cell-wall conically thickened at the apex (after the style of many teleutospores of *Uromyces* or *Puccinia*), and are provided with downward-turned spines which are larger in the lower half of the spore than towards the summit. They are in fact closely similar to *amphispores*. They are also accompanied by numerous capitate paraphyses. Furthermore, there is on *Anemone coronaria* an æcidium (*Æ. punctatum* Pers., *Æ. quadrifidum* DC.) accompanied by spermogones, which had hitherto stood isolated, not being followed by any other spore-form on the same plant. It occurred to Tranzschel, *reasoning merely from the similarity of the two teleutospores*, that this æcidium belonged to *P. Pruni-spinosæ* (24). The idea was without delay proved by experiment to be a fact, which has since been substantiated by other observers (3). Thus it is shown that *P. Pruni-spinosæ* is a heterœcious species, having its spermogones and æcidia on *Anemone* and its uredo- and teleutospores on *Prunus*.

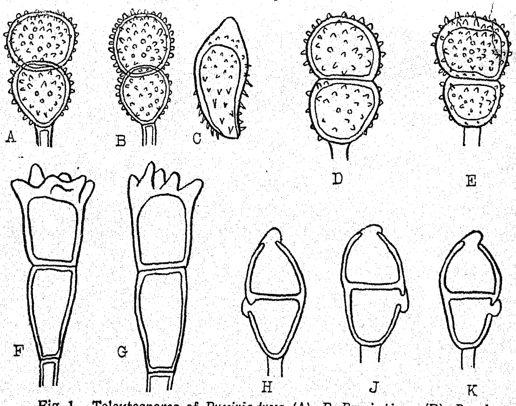


Fig. 1. Teleutospores of *Puccinia fusca* (A), *P. Pruni-spinosæ* (B), *P. cohæsa* (D), *P. Thalictri* (E), *P. coronata* (F), *P. Mesnieriana* (G), *P. albescens* (H), *P. Adoxæ* (J), and *P. argentata* (K), and Uredospore of *P. Pruni-spinosæ* (C). D is from an original specimen collected by Long. H, J, and K are selected specimens, but are fairly representative of each type. A to G, × 660; H, J, K, × 900.

To explain this state of things it was suggested that there was originally a complete autœcious species of *Puccinia* which had its spermogones, æcidiospores, uredospores and teleutospores on *Anemone*. From this, we may suppose, there could arise (1) a species of Micropuccinia on the *Anemone* with teleutospores only, the other two useful spore-forms being suppressed, but the useless [1] spermatia still lingering as a survival or legacy from the past, (2) a species which still retained its spermogones and æcidia on *Anemone* but which had transferred its uredo- and teleutospores, by a sudden mutation, to various species of *Prunus*.

Putting aside, for the moment, the consideration of the reasonableness of the suggestion, the possibility of such an evolution cannot be gainsaid. The mutation is possible, because the æcidiospores, being produced in enormous numbers at a certain period, must be spread over all the leaves of plants belonging to the same association within a certain radius; there they might germinate, the germ-tube would penetrate through a stoma if it could, and having once gained access to the stores of nutriment contained in the cells within would draw upon them for its food supply, if their mutual chemical and vital attractions and repulsions would permit it to do so. Untold millions of æcidiospores go through this experience annually, and untold millions fail; but that is no reason why, at rare intervals, when every circumstance is favourable, one of them should not succeed in establishing itself upon the new host. It is known that the æcidiospore is rejuvenated by the effect of the presence in it of two non-sister nuclei, and as Olive says (20) we should expect the heterœcism to arise, if at all, just at that point of greatest vigour. It is also known that germ-tubes can enter the stomata of plants other than their proper hosts (13): their further growth would demand a certain chemical affinity in the cell-contents of the two hosts, and probably also a slight change (mutation) in the cell-contents of the spore itself, such as we know, from Marshall Ward's experiments on *Puccinia dispersa*, to occur at intervals.

So far, however, this is mere supposition: but there is more to follow. If the imagined autœcious species on *Anemone* ever existed, it might still remain, in some corner of the world, if not in Europe. There *is* a very rare species, first described in 1902, on *Anemone decapetala* in Texas but found nowhere else, which answers

[1] All the numerous attempts that have been made to convey infection by means of the spermatia have uniformly failed.

to the exact requirements. This is *P. cohæsa* Long. Its spermogones and æcidia agree in every detail with those on *Anemone coronaria*, e.g., among other resemblances, in both the spermogones are similar in shape and distribution, and the margin of the æcidial cups breaks up into a few (usually four) spreading lobes—a very unusual circumstance from which *Æ. quadrifidum* derived its name. Its uredo- and teleutospores (Fig. I, D) agree equally with those on *Prunus*, the sori are the same in size and arrangement, both kinds of spores have the same unusual shape and the same surface markings, and the uredospores are accompanied by numerous capitate paraphyses. Finally, there is one particular detail of agreement which must convince the most cautious—the teleutospores of both occur in bunches of 10—20 together, all attached by short fragile pedicels to a common base. Arthur includes both species (*P. cohæsa* and *P. Pruni-spinosæ*), on this and other grounds, in his genus *Tranzschelia* (I). It is probable, though no investigation has been made, that in these cases the teleutospore-mother-cells bud off in succession from a common basal cell, as takes place in a smaller degree in *Leptinia* and *Chaconia* (15) and, as shown by Hoffmann (14), in *Endophyllum*, and by Dittschlag, in *Puccinia Falcariæ* (10).

Such a wonderful series of congruences suggests at once a reasonable explanation. *P. cohæsa* represents the original species. From this *P. fusca* arose by a shortening of the life-history (by dropping out some of the spore forms), a process which is now well known to indicate an adaptation to an environment in which the saving of time is of importance, as in Alpine districts or on early spring vegetation, such as in the case of *Anemone*. In Switzerland the percentage of Micropucciniæ is twice as great in the Alpine as in the lowland regions; the same is true of the flora of Sweden when compared with that of Germany (12). Secondly, *P. Pruni-spinosæ* arose by a sudden transference of the uredo- and teleutospore phases to another host, as outlined above. In this we can trace an agreement with Dietel's "Law." He arrived at the conclusion (9), by studying the sequence of the Uredineæ, that they have evolved *pari passu* with the plants upon which they are parasitic and, as a corollary, that when a mutation took place, leading to a change of host, it was almost always in the direction of selecting the new one from a group of later (or at any rate, not of earlier) evolution than the original host. In consonance with this is the fact that the Rosaceæ, to which *Prunus* belongs, are of a more specialised type than the Ranunculaceæ, to which *Anemone* belongs.

It is true that there are several apparent exceptions to the "Law," as in *Gymnosporangium*, which has its æcidial stage on Rosaceæ and its teleuto-stage on the Junipers. The "Law" is, in fact, only an empirical, but widely applicable "Rule."

Again, there are other Micropucciniæ which have teleutospores of exactly the same type as *P. fusca*, viz., *P. suffusca* Holw., on other species of *Anemone*, and *P. Thalictri* Chev. (Fig. 1, E) on species of *Thalictrum*, in Europe and North America—and on the other hand æcidia of the same type as *Æ. punctatum* and considered as equally belonging to *P. Pruni-spinosæ* have been found in North America on *Thalictrum* and *Hepatica* (1). All these are survivals from one ancestral species which at one time ranged widely over Ranunculaceæ of the tribe Anemoneæ, and of which we can predicate that it was autœcious, had all four spore-forms, the æcidia with a broad usually four-cleft margin, the uredospores thickened at the summit and more echinulate below than above, the teleutospores of two globose cells which separated easily and were adorned with numerous prominent and coarse warts, and possibly had its teleutospore-mother-cells produced in large clusters by budding from a common base. The remarkable fact is that, apart from the species here mentioned, these spore-characters are met with in the genus *Puccinia* only very rarely, and never all associated in this same way.

P. coronata and its close ally *P. Lolii (P. coronifera)*, which are known from all parts of the world except Africa, afford another instructive, though not equally convincing, example. Here we have a species[1] having its æcidia (spermogones appear to be wanting) on *Rhamnus*, and its uredo- and teleutospores on *Holcus* and other grasses. The teleutospores (Fig. 1, F) have at their apex a number of finger-like processes which impart to them an unusual appearance; *P. coronata* var. *himalensis* Barcl. (from Simla) has its æcidia on another species of *Rhamnus* and its fingered teleutospores on another grass *(Brachypodium)*. On *Rhamnus* there are two species of *Puccinia* which have teleutospores only, *P. Mesnieriana* Thüm. (Fig. 1, G) from Portugal, Teneriffe, Syria and California, and *P. Schweinfurthii* Magn. (from Abyssinia and tropical East Africa). These are the only two known on *Rhamnus*, and *both of them have teleutospores exactly like those of P. coronata*. An autœcious species on *Rhamnus*, having both æcidiospores and teleutospores, has not yet been met with; and the curious shape of the teleutospores, though very striking, is not without parallels in other not

[1] *P. coronata* and *P. Lolii* are merely "biologic" races of one species.

closely connected cases, e.g., *P. Festucæ* Plowr., with its æcidia on *Lonicera*, and *P. Beckmanniæ*, as well as species of *Uromyces (coronatus, phyllodiorum*, etc.). Nevertheless, the series of forms given above on *Rhamnus* and grasses bears a close similarity to that on *Anemone* and *Prunus*. If the same explanation is to apply, one must remember that the Gramineæ (and also the Cyperaceæ) are not, as has sometimes been thought, primitive families but more recently evolved ones, being derived like the Orchidaceæ from the Liliaceous type, though by different routes.

We find much the same relations existing in other groups of species; not to labour this point, I will refer briefly to two alone. The well-known *P. graminis* has its æcidia and spermogones on *Berberis*, and its uredo- and teleutospores on grasses all over the world. *P. Berberidis* Mont., from Chile, has æcidiospores and teleutospores on *Berberis; P. Meyeri-Alberti* Magn. from Chile and Patagonia, also on *Berberis*, has probably teleutospores only, which differ from those of *P. Berberidis* merely in having a greater length. The æcidia of *P. Berberidis* are not unlike those of *P. graminis*, but in the former case teleutospores are produced round the æcidial cup, obviously from the same mycelium (6.) There is also *P. Arrhenatheri* Erikss. (from Europe and Western Asia) which has its spermogones and æcidia on *Berberis* and its uredo- and teleutospores on *Arrhenatherum elatius*. The teleutospores of this species are similar to those of *P. graminis*, but on *Berberis* its perennial mycelium causes witches'-brooms, while the æcidium of *P. graminis* does not. Mention must also be made of *Æcidium Maghellanicum* and *Æ. Jakobsthalii-Henrici*, both on *Berberis* and from the antarctic regions, of which *Æ. Maghellanicum* causes no witches'-brooms, but the other does; their teleutospores are unknown. All these may be descendants of one ancestral autœcious species which grew on *Berberis* and of which the uredo- and teleutospore phases migrated to the Gramineæ, again without violating Dietel's "Rule."

The second instance is that of *P. Caricis*, which has its æcidium on *Urtica* and its teleutospores on *Carex*. Here also we find a Micropuccinia on *Urtica (P. Urticae* Barcl., from Simla) which has teleutospores only, similar to those of *P. Caricis* but occurring in dense clusters on coloured spots like those made by the mycelium of the æcidium of the latter on *Urtica*, and therefore, in a manner quite unlike the teleuto-sori of *P. Caricis*. In this connection it may be as well to call attention to the fact that, in many cases, the form of the sori and the colouring of the spots on

which they stand are determined by the nature of the host rather than by that of the parasite. The chief guide in classification must always be the *form* of the teleutospore. Dietel's "Rule," it will be observed, is again not broken.

PUCCINIÆ ON ADOXA.

Another case of a highly involved, but slightly different, nature must now be considered. On *Adoxa Moschatellina* in this country (a *spring* flowering plant) there is found an æcidium, accompanied by spermogones and sometimes followed on the same plant by a few scattered teleutospore-sori which contain also a small number of uredospores; this is called *P. albescens* Plowr. (Fig. 1, H), There is also found on the same host a *Puccinia* (*P. Adoxæ* Hedw. f.), which produces only teleutospores in densely crowded sori (Fig. 1, J). These two forms appear to be almost always separated: one attacking *Adoxa* in one district, and the other in another district, not only so in England, but also on the Continent. Moreover, these teleutospores of *P. Adoxæ* begin to appear abundantly in early spring (March) at the same time that the æcidia of *P. albescens* are appearing in their district, while the few teleutospore-sori of the latter do not appear till May. Thirdly, there is a *Puccinia* (*P. argentata* Wint.) which has its spermogones and æcidia on *Adoxa*, but its uredo- and teleutospores (Fig. 1, K) on *Impatiens;* these latter have been found in only one district in this country. The heterœcism in this case has been fully demonstrated by Bubák (4). The teleutospores of all three are almost exactly alike, and although an attempt has been made by Bubák to distinguish the two æcidia by the colour of the spores, the distinction is of little value, even if not, as I am inclined from my experience to think, quite untrue. Some authors unite the two former species, but this does not meet with general approval, and the most natural conclusion from the known facts is that we have here a mutating species which has not yet completely specialised itself into three forms—*P. albescens*, a complete autœcious species on *Adoxa* (Auteupuccinia); *P. argentata*, a Hetereupuccinia on *Adoxa* and *Impatiens*; and *P. Adoxæ*, a Micropucccinia on *Adoxa*.

The first of these would in that case represent the original form, from which the other two are being evolved. In North America, an æcidium on *Adoxa* is found, but the teleutospores are, at any rate, excessively rare on that plant (there seems to be only *one* record), while those on *Impatiens* are common. It appears reasonable to suggest that the fungus is becoming specialised as heterœcious in North America, where *Impatiens* is abundant, while

it is continuing to be autœcious in this country, where *Impatiens* is very rare, although it is at the same time evolving here a Micropuccinia which has not yet been found in America. We have, in fact, a case parallel to that diverse evolution of the biological races of *P. graminis* which is taking place at the present time in three distinct directions in Europe, North America and Australia respectively.[1] Whether the Balsaminaceæ, to which *Impatiens* belongs, are to be considered as of a higher type than *Adoxa* is a matter about which there might be two opinions, if *Adoxa* is placed among the Caprifoliaceæ; personally I should have little hesitation in putting the Balsam, with its complicated floral and fruiting mechanism, far above the simple little Moschatel.

Sub-divisions of Puccinia.

Before we conclude that the theory suggested by these examples (which might be largely increased) is fully justified, there are other aspects of the question to be considered. It is obvious that the great genus *Puccinia*, comprising now about 1,300 described species, must sooner or later be divided—whether into sections, sub-genera, or genera, matters not. Even in the 130 species of our British flora, some sub-division is necessary for the sake of clearness. Four attempts at such arrangements have been made. Schröter (22) instituted the sections Eupuccinia, Pucciniopsis, Brachypuccinia, Hemipuccinia, Micropuccinia, and Leptopuccinia, based upon the number and nature of the spore forms known. Thus, designating spermogones by O, æcidia by I, uredospores by II, and teleutospores by III, his sections may be defined (in the light of our present knowledge) as follows :—

Possessing		
O, I, II, III	Eupuccinia	Auteupuccinia, all on the same species; Hetereupuccinia, O and I on one species, II and III on another.
O, I, III	Pucciniopsis.	
O, II, III	Brachypuccinia.	
II, III	Hemipuccinia	Possibly most (though not all) of these will be found in the future to be heterœcious.[2]
[O] III	Micropuccinia	Spermogones not always occurring.

[1] In Australia, according to McAlpine (17), *P. graminis* has completely lost the power of infecting the Barberry, which is not a native of that country.

[2] It would seem possible to determine whether a supposed Hemipuccinia belongs to a heterœcious species or not, by cytological investigation. If the first-formed mycelium of the uredo-stage is binucleate, the fungus in question must be a stage of a heterœcious species: if not, if the binucleate condition arises in the course of development of the uredo, then it is a true Hemipuccinia. Of the fourteen species included under this head in Plowright's Uredineæ (21), five have been already proved to be heterœcious, and three others are strongly suspected to be so.

The Leptopucciniæ are omitted: there is not a special group of that kind. Schröter defined it as the group in which there are teleutospores only which germinate as soon as mature. But this is not absolutely true; most, if not all, the Leptopucciniæ possess spores of both kinds, some which germinate at once, and others which do so only after the winter's rest, e.g., *P. Veronicarum*. We should speak of lepto-forms of the groups: e.g., *Endophyllum Sempervivi* is a lepto-form.

Since this classification depends upon the number of known spore-forms, it is evident that a species must be changed from one section to another as our knowledge of it increases, e.g., *P. Pruni-spinosæ* was to Schröter a Hemipuccinia, now it belongs to the Hetereupucciniæ, while *P. cohaesa* belongs to the Auteupucciniæ and *P. fusca* to the Micropucciniæ. Schröter's classification does not indicate affinity in any degree; its sections cannot have the force of sub-genera.

Another more recent attempt at classification is that of the brothers Sydow (23). They arrange the species according to their hosts, beginning with those on the Compositæ and ending with those on the Gramineæ. In passing, there should be noted the false implication that the Compositæ are the most highly evolved order and the Gramineæ the least so. Here also allied species are occasionally widely separated, e.g., *P. fusca* and *P. Pruni-spinosæ*, though *P. fusca* and *P. cohæsa* are brought close together. Their method is excellent as an index, and is, indeed, employed by them on that ground; but it cannot be used in any other way, although it does in a large number of cases bring allied species together, simply because many of those parasitic upon allied genera or species have been evolved *pari passu* with the latter from a common ancestor respectively.

A third attempt is that of Fischer (12), who takes the form and markings of the teleutospore as his basis, but combines it with the grouping of the parasites according to their teleutospore hosts, or with the biological distinctions of Schröter. This is a great advance, because it brings together allied species, not only in the case of *P. fusca*, *P. suffusca*, *P. Thalictri*, but in many others; even if the heterœcism of *P. Pruni-spinosæ* had been known in time, however, it might still have been separated from its allies.

A fourth attempt is that of Arthur (1), who bases his genera, e.g., *Tranzschelia*, upon the number of spore-forms known combined with other morphological characters. This is also an

approach to the ideal classification, but it is subject to the same fatal objection as Schröter's. Arthur, for instance, separates *P. fusca* from *P. Pruni-spinosæ*, placing it in his genus *Polythelis*, though he brings *P. cohæsa* and *P. Pruni-spinosæ* together. If a method of classification is only correct in so far as it coincides with the groupings that have originated in a line of descent, then no such method can be satisfactory that does not place these three species in a common genus.

Dietel's Rule.

To illustrate Dietel's "Rule," we may consider the numerical relations of the species of *Puccinia* and *Uromyces* (the two highest evolved genera of the Uredineæ) to their hosts. The number of Dicotyledons in the world is to the number of Monocotyledons about as 5 : 1; the number of Pucciniæ parasitic on Dicotyledons is to the number on Monocotyledons about as 2 : 1; in the genus *Uromyces* the proportion is about the same (23). In other words, the distribution of the parasites has not yet attained so great an extension on the higher class as on the lower. The evolution of the parasites naturally lags behind that of the hosts.

The species of Pucciniæ on the Compositæ number over 300, *i.e.* nearly one-quarter of the known total. In Britain the number on Compositæ is also about one-quarter of the British Pucciniæ. The species of *Uromyces* on Leguminosæ number about 120 out of over 500 in the world; *i.e.*, again about one-quarter: the proportion in Britain is much the same. If the species of *Uromycladium*, all on *Acacia*, are included (and this genus differs from *Uromyces* mainly in bearing its teleutospores not singly, but in clusters upon a common stalk) then the world-proportion would be over one-quarter. The striking point is that the greatest number of each genus lives on orders belonging to the largest and most highly evolved sections of the gamopetalous and polypetalous groups respectively. *Puccinia* seems to have specialised upon the Compositæ in colder lands, and *Uromyces* upon the Leguminosæ in warmer lands, for the species of *Puccinia* on the latter are hardly more than 1%, and of *Uromyces* on the former about 6%, of the totals.

The number of *Pucciniæ* on the Grasses is about 150, and of *Uromyces* about 50; *i.e.*, in each case in the neighbourhood of 10%. The relations of the numbers of these genera to other families are equally interesting, but would take too long to unravel here. It is worthy of mention, however, that there are few on the Rosaceæ,

and none at all on the Salicaceæ or the Coniferæ, though Uredineæ of lower type are frequent on those Orders. This shows that, as the more specialised orders of angiosperms arose in the course of evolution, fresh parasites of a higher type were evolved to suit them.

Spore-Forms and their Relations.

In speaking of the Micropucciniæ so far, it has been assumed that the existence of species with *one* spore-form arose by suppression of the others. But reduction alone is never capable of providing a full explanation of the evolutionary process; there must always have been an advance in complexity first. If we consider Schröter's classification we see that the one spore-form which runs through the whole series is the teleutospore (including, of course, the basidiospore which is its invariable product); this is present in every case, whatever else may be absent.[1] It is natural to conclude that this is the essential and ancestral type of spore.

But if the theory of Blackman and others that the æcidium represents a remnant of a formerly existing sexual process is accepted, as it must be, then a spore produced like the æcidiospore must also be one of the ancestral types.

Again, there are many grounds for assuming that the æcidiospores, uredospores, and teleutospores (and even the spermatia as well) are all modifications of one common spore-form. The formation of spermatia in the spermogone takes place much in the same way as that of æcidiospores in the æcidium, except that there are no intercalary cells. In certain cases *primary* uredospores take the place of æcidiospores, being followed by *secondary* uredospores, alike in form but differing in the character of the sorus, and probably in all such cases the primary uredospores alone are accompanied or preceded by spermogones, as in *P. obtegens*. Another species, *P. Podophylli*, has primary and secondary æcidiospores, the latter taking the place and function of uredospores. In *Uromyces Veratri* similar spores, if sown upon young leaves produced only uredospores; if on old or sickly leaves produced more teleutospores (18). It is well-known that teleutospores are commonly borne upon the same mycelium as uredospores; but also æcidiospores can be followed by teleutospores upon the same

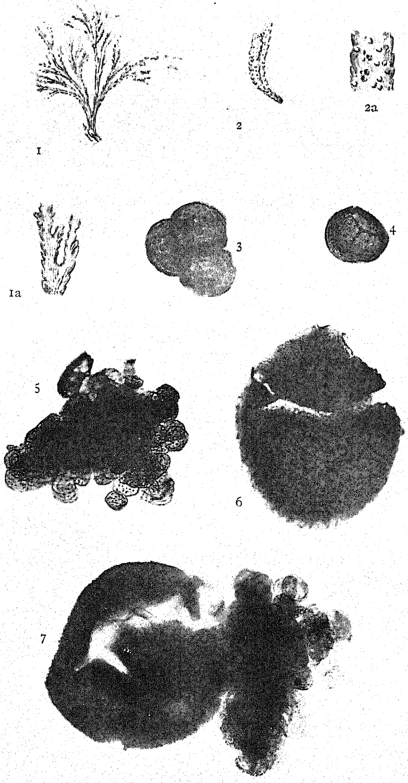
[1] Isolated "species" of Uredo and Æcidium are ignored, because there is reason to believe that all, or nearly all, of these will be assigned to other species as our knowledge of them increases. Of the 38 "imperfect species" recorded in Plowright's Uredineæ, only four are now still unassigned.

mycelium, even within the æcidial cup, as in *U. Cunninghamianus* (2), or close to its margin, as in *Puccinia Berberidis* (6), or in a circle round it, as in *Uromyces Behenis*. The pedicel of the uredo- and teleutospore is the homologue of the intercalary cells of the æcidiospore-chain. In the sori of the primary uredospores of *Phragmidium Potentillæ-canadensis* (= *Ph. Tormentillæ* Fckl.) the basal cells act as in the formation of æcidiospores, but the lower sterile half of the spore-mother-cell, instead of disintegrating, elongates to form the pedicel of the uredospore. Large basal cells, similar to those occurring in the æcidium, are frequently found in the sori of uredo- and teleutospores. In many of the lower Uredineæ those two kinds are produced in chains. In *Chrysomyxa*, æcidio-, uredo-, and teleutospores are all concatenate. We have thus various requirements to be satisfied by any explanation of the origin of these spores: is it possible to reconcile them all?

Endophyllum.

The genus *Endophyllum* comes to the rescue, especially since the recent investigations of Hoffman (14). He shows that *Endophyllum Sempervivi* has only one kind of spore in addition to the spermatia and basidiospores. This is produced in a cup exactly like an æcidium, in chains with intercalary cells, from a basal fertile cell with two nuclei, which arises as in *Phragmidium*, etc., by the fusing of two of the cells of the fusion-tissue after the manner described by Christman (5); the two which fuse are adjoining cells of the same mycelium (not situated in any definite plane), but presumably never of the same hypha. The pair of nuclei then divide in the well-known conjugate way, the æcidiospores thus all containing at first two non-sister nuclei which afterwards fuse as the spore approaches maturity. This fusion has been denied by Sapin-Trouffy and Maire, but evidently as the result of mal-observation: their mistake has led to several unfounded conjectures about *Endophyllum*. The æcidiospore germinates as soon as mature with a basidium and basidiospores, like an ordinary teleutospore of *Puccinia*, the fusion-nucleus having sooner or later divided twice, the first being the reduction-divivision. The spores of *Endophyllum Euphorbiæ* do the same.

Obviously these spores are at once æcidiospores by the mode of their formation, and teleutospores by the mode of their germination. Here, then, is one at least of the ancestral types of spore among the higher Uredineæ; the lower group, the Melampsoraceæ, which



London Stereoscopic Co. imp.

SELAGINELLITES DAWSONI sp. nov.

SEWARD—A BRITISH FOSSIL SELAGINELLA.

demands a separate treatment, is excluded from present consideration. It should be noted that, even before its nuclear history was properly investigated, *Endophyllum* was rightly considered to be one of the highest forms of the lower group or of the lowest forms of the higher group, if with Dietel we suppose the Uredineæ to consist of two groups, the Pucciniaceæ and the Melampsoraceæ, or, as I have named them, the Pedicellatæ and the Impedicellatæ. Moreover, Hoffmann shows that the basidium of *E. Sempervivi*, sometimes bears more than one basidiospore from each of the four cells. He observed as many as eight from one basidium. We may conclude that this is the primitive mode of basidiospore-formation, resembling in that respect that of the Ustilagineæ, from the ancestors of which it is generally agreed the Uredineæ are descended. I have not been able to meet with this mode in *E. Euphorbiæ*; in that species, so far as I have seen, there is always one basidiospore on each of the four cells. Müller's experience seems to be the same (19).

We may now take it as established that *Endophyllum* approaches the form of the primitive Pucciniacea, though undoubtedly it has a more highly developed peridium. The latter, therefore, had on the same mycelium spermogones producing male spermatia, and female cells arranged in a more or less cup-shaped chamber. At some time or other, either before or after this, fertilisation by the spermatia was lost, and the conjugation of two equal female gametes took its place. The resulting spores were produced in chains, with intercalary cells to facilitate dispersal—these on germination produced a basidium and basidiospores, each of which could infect the host again, and produce a mycelium which again bore spermogones and æcidia. Hoffmann proved that this is so in the case of *Endophyllum Sempervivi*. It may be noted that in the Ustilagineæ there is, in addition to the conidia, only one kind of spore which acts like the teleutospores of the Uredineæ.

The sterigmata of *Endophyllum* are variable in size and indefinite in shape. This is itself a sign of a lower stage of evolution; in the higher types of the Uredineæ the basidium was modified so as to produce only one basidiospore from each cell of the basidium and on a well-defined sterigma. The life-cycle of *Endophyllum* may be represented diagrammatically, much as is done by Hoffmann, in the following scheme;—

Gametophyte
Basidiospore
|
Mycelium
/ \
Æcidium Spermogone
| |
Female cell Spermatium
\\
Sporophyte
Fusion cell
||
Spore-mother cell
// \\
Intercalary cell Spore
Λ
o o
Λ Λ
o o o o
Basidiospores

This hypothesis of the primitiveness of an *Endophyllum*-like Uredine was propounded by Barclay (2) but, since in his day the nuclear history of the Uredineæ had not been at all investigated, it was devoid of that strong confirmation which the researches of Hoffmann have now afforded it. Barclay shows how, in *Uromyces Cunninghamianus*, only the primary æcidiospores are accompanied by spermogones; these æcidiospores, when mature, germinated sometimes by a kind of abortive basidium which became uni-septate, but instead of producing basidiospores each cell gave rise to a germ-tube[1], which would enter the host (presumably through a stoma) and there produce a mycelium which would give rise to the secondary æcidiospores; these might then repeat the process or *be followed within the same cup* by teleutospores.

This enables us to picture exactly how the first step of the separation of teleuto– from æcidiospores could originate; the transformation of these secondary æcidiospores into uredospores would then be a simple change. It must be remembered that the spores of *Endophyllum* germinate at once; on that account the fungus hibernates by its mycelium in the growing points of the host, a comparatively inefficient method. The separation of æcidio- from teleutospores, and the consequent intercalation of spores devoted entirely to the spreading of the parasite, would enable the teleutospore more easily to become a resting spore, and thus increase the ability of the fungus to adapt itself to fresh conditions. The

[1] When teleutospores germinate in water, deprived of air, they generally produce long tubes, and not infrequently no basidiospores.

intercalation is, as was to be expected, a lengthening of the sporophytic generation.

When the sporophytic generation was still further lengthened, by the introduction of uredospores, it is certain that, of those which had all the three spore-forms, the autœcious species would be first evolved. There are then three possible hypotheses by which the origin of heterœcism could be explained. The *first* is due to Dietel, (7) and agrees with the one suggested at the beginning of this article. It is approved by Klebahn (16). The *second* is Dietel's later alteration of his hypothesis (8) : he supposes that the primitive form of any group of species possessed only teleutospores, and was confined to one host: the present state of things arose (1) by intercalation, (2) by an accompanying mutation signified by the migrating of the æcidiospores on germination to a new host. This is also incorporated in the hypothesis here advocated, although in a sense not conceived by Dietel. The *third* is due to Fischer; (11) he supposes that the primitive form was plurivorous and possessed all spore-forms: then a further development took place by which some of the evolved species restricted certain of their spore-forms to hosts of particular families and the others to hosts of other families (*i.e.*, became heterœcious), while at the same time by suppression of some of the spore-forms Micropucciniæ and Brachypucciniæ arose. Thus, to return to the case of *Puccinia fusca* and its allies, the primitive form would be supposed to possess all spore-forms and to occur with all of them indiscriminately on Anemoneæ and Pruneæ. While certain abnormal cases might, perhaps, be more easily explained on this hypothesis, it labours under several difficulties. In the first place, it affords no explanation of Dietel's "Rule," and in the second there does not seem to exist a species of Uredineæ which is plurivorous in the required sense, *i.e.*, has all its spore-forms equally and indiscriminately on hosts belonging to diverse families. While the other hypotheses do not explain all the known cases, *e.g.*, that of *Puccinia Isiacæ* [1] or *Uromyces Scirpi*, they can, at any rate, as shown above, present actual instances of existing species which satisfy the theoretical requirements.

[1] *Puccinia Isiacæ* has its teleutospores, so far as is known, on *Phragmites* alone, but its æcidia have been produced by Tranzschel on twenty-one plants belonging to nine widely different families, ranging from Cruciferæ to Scrophulariaceæ. Manufactured instances, however, are not much to the point.

The views here put forward concerning the evolution of the Uredineæ are expressed diagrammatically in the accompanying figure (Fig. 2).

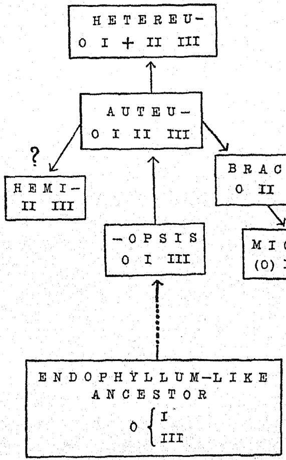


Fig. 2. Diagram representing the Evolution of the higher Uredineæ.

EXPLANATION. The prefixes and suffix can be applied to any genus. Taking *Puccinia* as an example: Pucciniopsis represents the stage when the primitive æcidio-teleutospore is divided into two spore-forms, an æcidiospore germinating conidially and a teleutospore germinating basidially; Auteupuccinia is an improvement upon this, because the intercalation of numerous generations of uredospores improves the facilities for dispersal; Hetereupuccinia is again an improvement, since in this case the fungus can form its spores upon hosts that completely disappear during the unfavourable period, if the alternate host survives; Brachypuccinia and Micropuccinia show adaptations in another way by shortening the development and quickening the formation of teleutospores, thus enabling the species to exist in subarctic or alpine regions—many Micropucciniæ still retain the spermogones, others have completely lost them; Hemipucciniæ are a mixed group, as explained in the text.

SUMMARY.

The conclusion at which I wish to arrive is this:—The primitive ancestors of the Pucciniaceæ possessed only one spore-form (æcidio-teleutospore) and were restricted to one host or to a series of closely allied hosts. From these arose cases like those of *P. Tragopogi* and *Uromyces Cunninghamianus*, where the æcidiospore germinated conidially and produced on its mycelium a

teleutospore which germinated basidially. Barclay's account shows how this may well have arisen. Such a change would tend to an increased spread of the parasite, for the basidiospores are the most delicate possible of spore-forms and the mortality among them must be enormous. In some experiments which I have recently carried out in the open with *Puccinia Caricis* (see Journ. Bot., 1913, p. 42), it is quite within the mark to say that scarcely more, than one or two in a billion basidiospores achieved their end in infecting the Nettle. A spore which germinates like an æcidiospore has *many more chances* of establishing itself upon its victim than one which produces basidiospores.

From this to the intercalation of uredospores is but a small step. In some species æcidiospores and uredospores are almost exactly alike in size and form. We know of cases where uredospores are few and rare; the steps to those instances where uredospores are numerous and form the chief means of fresh infection are many and abundantly represented. Such cases, which include many of the *Pucciniæ* on the Grasses, often belong to widely distributed species. One can even conceive of a state of things (largely perhaps dependent upon climate) where the fungus relies entirely upon uredospores for its existence, and loses altogether the other spore-forms, at first functionally and at last morphologically. The Black Rust of Wheat (*P. graminis*) in Australia and *Uromyces Fabæ* in Ecuador seem to be approaching such a condition.

So far the fungus is considered to be autœcious. The formation of the heterœcious habit demands, on this hypothesis, a sudden, but not inconceivable mutation, of which evidence will yet be found From the complete autœcious species, on the other hand, Brachy- and Micro-forms might easily arise by the dropping out of some of the spore-forms as occasion demanded.

The reverse process of forming autœcious species with all spore-forms from those having only teleutospores of the type of *P. Ægopodii* (which has no spermogones), as imagined by Dietel in his second hypothesis, would imply the introduction of functionless gametes separately on each such occasion. The very persistence of the occurrence of the useless spermatia in so many species is a proof of their deep underlying primitiveness, and no hypothesis of the evolution of the higher Uredineæ is tenable which does not start with the existence of them and of the correlative female cells.

The Botanical Laboratory,
University of Birmingham.

LITERATURE REFERRED TO.

1. Arthur, J. C. "North American Flora, vol. vii., parts 2, 3, Uredinales." (1907-12).
2. Barclay, A. "On the Life-History of a remarkable Uredine on *Jasminum grandiflorum.*" Trans. Linn. Soc. Bot. iii. 141, pl. 49-50 (1891).
3. Brooks, F. T. "The Life-History of the Plum Rust in England." NEW PHYTOLOGIST, x. 207 (1911).
4. Bubák, F. "Infektionsversuche mit einigen Uredineen." Centralbl. für Bakter, 2, xii. 411 (1904).
5. Christman, A. H. "Sexual Reproduction in the Rusts." Botan. Gaz., xxxix. 267 (1905).
6. De Bary, A. "*Æcidium abietinum*" (with note on Puccinia Berberidis). Botan. Zeitung, xxxvii. 845-7, pl. 10, f. 9 (1879).
7. Dietel, P. "Beiträge zur Morphologie und Biologie der Uredineen." Botan. Centralbl. xxxii. 183 (1887).
8. ,, "Waren die Rostpilze in früheren Zeiten plurivor?" *ibid.*, lxxix. 81 (1899)
9. ,, "Betrachtungen über die Vertheilung der Uredineen auf ihren Nährpflanzen." Centralbl. für Bakter., 2, xii. 218 (1904).
10. Dittschlag, E. "Zur Kenntnis der Kernverhältnisse von *Puccinia Falcariæ.*" Centralbl. für Bakter., 2, xxviii. 473 f. 29 (1910).
11. Fischer, E. "Entwicklungsgeschichtliche Untersuchungen über Rostpilze." Beiträge zur Kryptogamen-Flora der Schweiz, i (1898).
12. ,, "Die Uredineen der Schweiz." (1904).
13. Gibson, C. M. "Notes on Infection Experiments with various Uredineæ." NEW PHYTOLOGIST, iii. 184 (1904).
14. Hoffmann, A. W. H. "Zur Entwicklungsgeschichte von *Endophyllum Sempervivi.*" Centralbl. für Bakter., 2, xxxii. 137 (1911).
15. Juel, H. O. "Die Ustilagineen und Uredineen der ersten Regnell'schen Expedition." Bihang till K. Svenska Vet.-Akad. Handlingar, xxiii. Afd. 3, no. 10 (1897).
16. Klebahn, H. "Die wirtswechselnden Rostpilze." (1904).
17. McAlpine, D. "The Rusts of Australia." (1906).
18. Morgenthaler, O. "Ueber die Bedingungen der Teleutosporenbildung bei den Uredineen." Centralbl. für Bakter., 2, xxvii. 73 (1910).
19. Müller, W. "Der Entwickelungsgang des *Endophyllum Euphorbiæ-silvaticæ.*" Centralbl. für Bakter., 2, xx. 333 (1908).
20. Olive, E. W. "Origin of Heterœcism in the Rusts." Phytopathology, i. 139 (1911).
21. Plowright, C. B. "A Monograph of the British Uredineæ and Ustilagineæ." (1889).
22. Schröter, J. "Kryptogamen-Flora von Schlesien." Band iii. (1889).
23. Sydow, P. et H. "Monographia Uredinearum." (1904-12).
24. Tranzschel, W. "Ueber die Möglichkeit die Biologie wirtswechselnder Rostpilze auf Grund morphologischer Merkmale vorauszusehen." Arb. Kais. Petersburg. Naturf. Gesell., xxxv. 1 (1904).

RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

BY F. CAVERS.

(Continued from p. 83),

OF the unicellular Chlamydomonadaceæ, *Chlorogonium* (Fig. 4, F, G, H) is probably on the whole the most primitive. In its elongated spindle-like form, this genus differs from the majority of the Volvocales, but an approach to the same shape is seen in *Carteria obtusa*, and the zoogametes of *Stephanosphæra* are spindle-shaped. In *Chlorogonium* the cell divides transversely to form a row of four daughter-cells, but these at once become elongated and slide past each other, acquiring the spindle form. Transverse division occurs in some species of *Chlamydomonas* (Fig. 4, B), though here, as in *Sphærella*, division is originally longitudinal and there is rotation of the dividing protoplast. In *Chlorogonium* the chloroplast is ill-defined and spongy and varies considerably in form, being in some cases ring-like or even spiral, hence symmetrical halving can be attained without the longitudinal division which is apparently essential in forms with a basin-shaped chloroplast; there are numerous (up to sixty) pyrenoids and about a dozen contractile vacuoles (Jacobsen, 61). *Cercidium* resembles *Chlorogonium*, but has only two pyrenoids and two vacuoles. Other simple forms are *Chlamydomonas* (Fig 4, A to D) and *Chloromonas*, the former with pyrenoids (typically one, but sometimes more) and the latter with none. Pascher's new genus *Agloë* (Fig. 4, E) is allied to these forms, but its chloroplast is peculiar in structure, resembling two conical flasks placed base to base and being H-shaped in optical section, with a pyrenoid in the middle of the transverse plate-like portion, and there are numerous contractile vacuoles. *Glœomonas* is an imperfectly known genus, probably allied to *Chloromonas* but with several chloroplasts. Various other genera have been described which probably represent offshoots from the *Chlamydomonas* type, though some of them are imperfectly known. Thus, *Coccomonas* (Fig. 4, J, K) appears to differ from *Chlamydomonas* chiefly in having a greatly thickened wall, often four-angled; *Pteromonas* (Fig. 4, L, M) is also thick-walled, the wall projecting as two lateral wings, as in the Carteriaceous genus *Scherffelia;* while *Phacotus* has a sculptured wall consisting of two loosely connected valves which separate to let the daughter-cells escape. Another elaboration is seen in *Brachiomonas* (Fig. 4, P, Q) and *Lobomonas* (Fig. 4, M, N); in the former the cell has a pointed posterior process and from its rounded anterior end there spring four recurved processes, in the latter the ovoid cell is produced into several rounded wart-like out-growths. In *Brachiomonas* (Fig. 4, R, S) the daughter-cells acquire the form of the parent before escaping (Teodoresco, 140; West, 147); as pointed out by

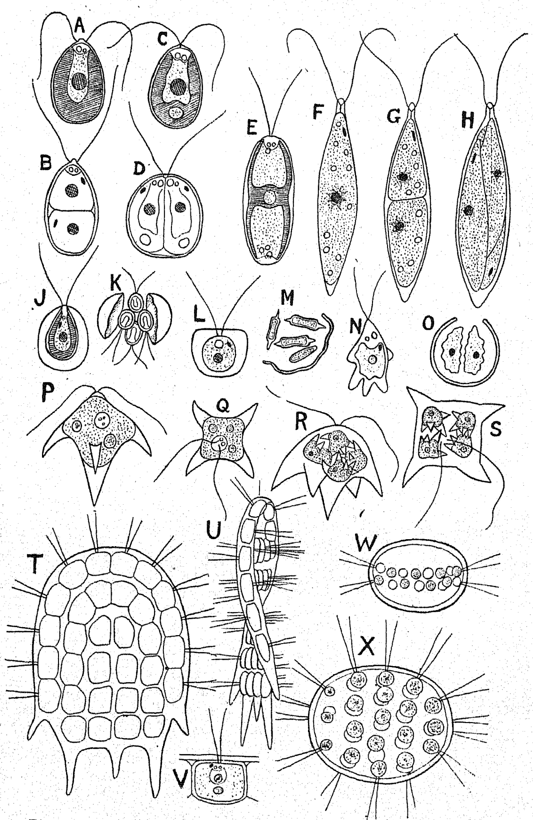


Fig. 4. CHLAMYDOMONADACEÆ. A, B, *Chlamydomonas* (*Chloromonas*) *variabilis* Dang.: this species has no pyrenoid; C shows transverse division. C, D, *Chl. Ehrenbergii* Gorosch. (longitudinal division shown in D). E, *Agloë biciliata* Pascher. F, G, H, *Chlorogonium euchlorum* Ehrb: in G the protoplast shows transverse division into two, in H the four daughter-cells formed by a further division have become arranged longitudinally within the mother-cell. J, K, *Coccomonas orbicularis* Stein: in K the wall of the resting cell has ruptured to set free the four daughter-cells. L, M, *Pteromonas alata* (Cohn) Seligo;

in M the liberation of the four daughter-cells. N, O, *Lobomonas Francei* Dang. P to S. *Brachiomonas submarina* Bohlin: P and R in side view, Q and S in anterior view; in R and S the formation of daughter cells. T to V, *Platydorina caudata* Kofoid: T, surface view; U, side view, showing the slight spiral twisting of the plate-like cœnobium; V, a single cell. W, *Stephanoon Askenasii* Schewk. X, *Pleodorina illinoisensis* Kofoid (the four small vegetative cells are shown at the left).

A to D, F to H, from Jacobsen; E, from Pascher; J, K, from Stein; L, M, from Wille; N, O. from Dangeard: P, Q, R, S, from West; T, U, V, X, from Kofoid; W, from Schewiakoff.

Fritsch (46) this recalls the autospore formation characteristic of the Scenedesmaceæ and Phytheliaceæ among the Protococcales. Included in the unicellular Chlamydomonadaceæ are two colourless saprophytic forms—*Polytoma* (Francé, 43; Prowazek, 117) which is probably derived from *Chlamydomonas*, and *Chlamydoblepharis* which resembles *Coccomonas*. In his recent classification of the Volvocales, Wille (150) includes in the Chlamydomonadaceæ the genera *Nephroselmis* and *Glœococcus*, but the former is better placed among the Cryptomonads, while the latter belongs to Tetrasporaceæ. Of the six genera appended by Wille to the Volvocales as doubtful forms, *Glœomonas* may be placed near *Chloromonas*, despite its possession of numerous chloroplasts; *Cylindromonas* and *Mesostigma* probably belong to Euglenineæ, and *Tetratoma* to Carteriaceæ; *Xanthodiscus* and *Kleiniella* are still imperfectly known, though Lemmermann (85) places the former in the Cryptomonadineæ, while Francé (43) regards *Kleiniella* as allied to *Coccomonas* and *Chlamydoblepharis*.

As pointed out by Fritsch (46), of the three attempts at cœnobium formation seen in the Volvocales, that represented by *Gonium* has alone proved successful and has given rise to the remarkably complete ascending series which culminates in *Volvox*. Schussnig (133) has recently described in detail the life history of *Gonium pectorale*, and has shown that in addition to the formation of daughter colonies and zoogonidia, reproduction occurs by means of aplanospores and by the conjugation of isogamous zoogametes; while Harper (54) has carefully studied the structure and division of the *Gonium* colony. Pringsheim's observation that *Pandorina* shows heterogamy does not appear to have been repeated by recent writers on the life history of this genus; while no further observations on the peculiar genus *Platydorina* (Fig. 4, T to V) have apparently been made since its discovery by Kofoid (70) and its life history is still unknown. Schewiakoff's genera *Mastigosphæra* and *Stephanoon* (126) appear to bridge the gap between *Pandorina* and *Eudorina*, though their life history is unknown. In *Mastigosphæra*, the cells, which have but one flagellum, are less closely packed in the spherical cœnobium than is the case in *Pandorina;* while in *Stephanoon* (Fig. 4, W) the cells are arranged on the equator of the cœnobium, as in *Stephanosphæra*, but in two alternating rows. In *Eudorina* the cells are spaced out at the periphery of the spherical cœnobium, though showing a tendency to be arranged in circles, but all the cells are alike capable of reproduction, whereas in *Pleodorina* and *Volvox* there is differentiation into vegetative and reproductive cells. Until recently, *Pleodorina* with two species—*P. californica* Shaw (138), *P. illinoisensis* Kofoid (69)—was known only from the United

States, but *P. californica* has since been discovered in Ceylon (Fritsch, 46), in France (Chatton, 27), and in Java (Woloszynska, 145), while *P. illinoisensis* has been found near Heidelberg (Merton, 92), and the life history of this genus has been worked out in detail by Chatton and by Merton. In *P. illinoisensis* (Fig. 4, X) the cœnobium consists of 32 (more rarely 16 or 64) cells, arranged in five circles, the two polar circles having four cells each and the other three circles eight cells each; the cells of the anterior polar quartette are vegetative only, never dividing to form new cœnobia and are smaller than the remaining cells. This species thus forms a transition from *Eudorina* to *Pleodorina californica*, in which the cœnobium consists of 64 or 128 cells and is sharply divided into an anterior hemisphere in which the cells are purely vegetative and only one-third to one-half as large as the reproductive cells of the posterior hemisphere. In *Pleodorina* the cells have two contractile vacuoles and numerous pyrenoids, and

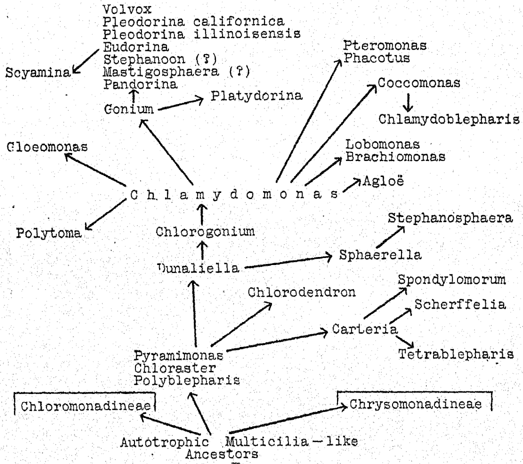


Table B.—Suggested Phylogeny of the Volvocales. For details, see Text.

the chloroplast is reticulate; in both species, oogamous sexual reproduction occurs as in *Eudorina*, any of the potentially reproductive cells producing either a mass of antherozoids, an oosphere, or a daughter-cœnobium. The two species of *Pleodorina* form perfect connecting links between *Eudorina* and *Volvox*, in which last genus the vast majority of the cells in the large cœnobium are vegetative and there is still more pronounced differentiation between

the vegetative and the reproductive cells and more marked oogamy, the oogonial cells being differentiated at an early stage in the formation of the cœnobium and having no flagella. Van Tieghen's genus *Scyamina* is an imperfectly known colourless form, in which the numerous cells are placed at different depths in the spherical cœnobium, instead of being confined to the periphery as in *Eudorina;* it is quite uncertain whether it represents a saprophytic offshoot from a *Eudorina*-like type, or a form derived from *Polytoma* by cœnobial development, or indeed whether it is rightly placed in the Volvocales at all.

The inter-relationships of the Volvocales, as here suggested, are indicated on the accompanying Table B.

VI.—The Chrysomonads.

Since the publication of Senn's compilation in 1900, much work has been done on the Flagellate forms included by him in the Chrysomonadineæ and Cryptomonadineæ. From the extensive recent literature of these forms, to which Pascher has been the largest contributor, it will suffice to select for mention certain results which are of special interest in connexion with the phylogeny of the Algæ. Various new genera have been added to those enumerated by Senn, and some modifications of the earlier classification have been suggested. Senn divides the Chrysomonadineæ into three families characterised respectively by the possession of a single flagellum (Chromulinaceæ), two equal flagella (Hymenomondaceæ), and two unequal flagella (Ochromonadaceæ). Scherffel (125) has shown that *Monas*, *Oikomonas*, and various other genera placed by Senn in the Protomastigineæ are better regarded as colourless forms derived Chrysomonads; for instance, they show precise agreement with normal coloured Chrysomonads in producing leucosin, in the mode of encystment, and in various cytological details. In describing a new species of *Gymnodinium*, a genus belonging to the simpler Peridiniales which have been regarded as derived from the Chrysomonadineæ (see below), Ohno (94) criticises the systematic value of the flagellum number in the classification of the Flagellata. This new species differs from all other Peridiniales in having two longitudinal flagella instead of one, in addition to the usual transverse flagellum, but otherwise must be placed in the genus *Gymnodinium*. The same objection has been raised with regard to the lower Green Algæ,[1] but Senn's classification is accepted by Pascher and other recent writers on the Chrysomonads, since (as in the case of the Green Algæ) the groups are distinguished by characters other than the number of flagella. In Pascher's suggested classification (99), the Cryptomonads are merged in the Chrysomonadineæ, which are divided into four orders. The first three of these (Chromulinales, Isochrysidales, Ochromonadales) coincide with Senn's three families of Chrysomonadineæ, while the fourth (Phæochrysidales) is characterised by the possession of laterally inserted flagella—in the other three orders the flagella are terminal—and includes the Cryptomonadineæ of Senn.

[1] See Review of Wille's classification of Green Algæ, by R.P.G., New Phytologist, vol. IX., 1910, p. 78.

The Chrysomonads are characterised by a peculiar endogenous method of cyst formation. Before a definite cyst appears, there is visible within the protoplast a membrane covered by an amœboid protoplasmic layer (Fig. 5, *11-14*), which produces sculpturing on the outer surface of the cyst membrane, but later this protoplasm retreats within the membrane through a pore which has been left, this pore being afterwards closed by a plug which in some cases consists of cellulose; the membrane usually contains silica. A similar method of cyst formation occurs in certain colourless heterotrophic genera which have hitherto been placed in the Protomastigineæ, and on this ground, as well as on account of other cytological resemblances, it is suggested that these forms should be transferred to the Chrysomonads. These forms, which may be regarded as colourless derivatives from normal autotrophic Chrysomonads—corresponding with the colourless forms (*Polytoma*, etc.) included in the Volvocales—belong to the genera *Monas*, *Oikomonas*, *Dendromonas*, *Antophysa*, *Cephalothamnion*, etc. It would appear that further investigations will lead to a considerable number of genera being transferred from the Protomastigineæ to the Chrysomonads, and doubtless to other groups of pigmented Flagellata, if we accept the view that where colourless and coloured Flagellates show close agreement in every character save the presence or absence of assimilatory pigments, the colourless forms are to be regarded as having arisen from the coloured as an adaptation to a heterotrophic mode of nutrition.

The recent work of Pascher, Scherffel, Senn, and others has shown that the Chrysomonadineæ (in the wider sense, as defined by Pascher) form a remarkably diversified group, in each order of which various parallel developments may be traced, starting from relatively simple free-living and usually small forms. The chief of these parallel developments are the formation of motile colonies analogous with those of the higher Volvocales, and of variously constructed non-motile colonies corresponding with those of the Tetrasporaceæ and other families of Protococcales characterised by aggregation of the cells into mucilaginous masses; the occurrence of amœboid forms and of amœboid phases, the latter perhaps to be regarded as reversions to an ancestral condition; the lobing, division and further elaboration of the primitively indefinite and reticulate or basin-shaped chromatophore; the coördination of the contractile vacuoles to form a pulsating vacuole system similar to that seen in the Chloromonadineæ and Eugleninеæ; the substitution of solid carbohydrate assimilates (paramylum and starch) for oil and leucosin; the elaboration of the outer protoplasmic layer into a firm periplast and finally into a definite membrane (in some cases consisting of cellulose) which may form either a close-fitting or an outstanding and cup-like perisarc; the outgrowth of tentacles from the periplast; and the development of sculpturings and of various excrescences (ridges, spines, etc.) on the cell-wall.

The Chromulinales include the simplest forms of the Chrysomonadineæ. In the lowest family, Chrysapsidaceæ, the cells are free-living and are amœboid; in *Chrysapsis* the chromatophore is an indefinite reticulate peripheral sheet, while in *Chrysamœba* and *Nannochrysis* it is basin-shaped, though in some species of *Chrys-*

amœba it becomes deeply bilobed and even divided into two (Fig.5, *1,2*). In *Chrysapsis*, division often occurs within a gelatinous investment, while in *Nannochrysis* the formation of a palmella-stage is more pronounced and several divisions occur before the products of division become free by dissolution of the jelly. These simple forms show marked resemblance to some of the simpler Protomastigineæ; *Chrysamœba* is very similar to *Mastigamœba* and *Oikomonas*, apart from the absence of a chromatophore in the latter genera.

The Chromulinaceæ, forming the largest family of Chromulinales, include solitary and colonial forms, the former showing a elaboration of the protoplast as compared with the Chrysapsidaceæ; there is usually a single basin-shaped chromatophore, but sometimes two or even more may be present. Among the solitary forms, *Chrysococcus* (Fig. 5, *15, 18*) has a thick shell or perisarc closely investing the periplast, but with a small anterior opening for the flagellum, the periplast of some species is ornamented with wart-like out-growths, and there is either a basin-shaped chromatophore or two lateral curved plate-like chromatophores, or several discoid chromatophores (Pascher, 99). A further elaboration is seen in the curious epiphytic genera *Chrysopyxis* and *Stylococcus*, in which the body is amœboid and lies freely within a goblet-like shell or perisarc which projects freely beyond it, and is produced at the base into a hapteron; longitudinal division occurs within the shell, and one of the daughter-cells escapes, produces a perisarc with an attaching process, and settles down; the cell contains cellulose, and the "flagellum" is in reality a "rhizopodium," or branched filamentous pseudopodium, at any rate in *Chryopyxis* (Fig. 5, *26-30*), which may be regarded as practically a *Chrysamœba* that has become epiphytic and produced a shell; in *Stylococcus* (Fig. 5, *23-25*), the "flagellum" is unbranched, but differs from the normal type of flagellum in being motionless and is doubtless pseudopodial.

The colonial genera of Chromulinaceæ show an advance upon the Chrysapsidaceæ, in that the palmella stage is more enduring, and in the genus *Hydrurus* becomes dominant. In *Chromulina Hokeana*, division occurs in the motile state, and the products of two or three successive divisions remain coherent to form a four- or eight-celled motile colony, comparable with the cœnobia of *Gonium* and *Pandorina*, and thus representing the "Volvocine tendency" which has appeared independently in several distinct groups of Chrysomonads. In most species of *Chromulina* (Fig. 5, *9-14*). however, division occurs in a resting palmella state (after the cells have lost their flagellum), giving rise to an indefinite mucilaginous mass; the free flagellate cells are amœboid and resemble *Chrysamœba*. A far more enduring and definite palmella state occurs in *Hydrurus* (Fig. 5, *37–41*); the motile cells ("zoogonidia") are of tetrahedral form, with the flagellum at the broader anterior end and on coming to rest lose the flagellum, become attached assume an ellipsoid form, secrete a mucilaginous stalk, and by repeated division give rise to an elaborately and regularly brancbed colony of considerable size. In this colony the cells are more crowded in the smaller branches than in the main axis and the larger branches; the whole structure behaves like a multicellular plant, growth in length depends on single apical cells, and the zoogonidia are produced from the branches, two or four arising by division of a parent-cell.

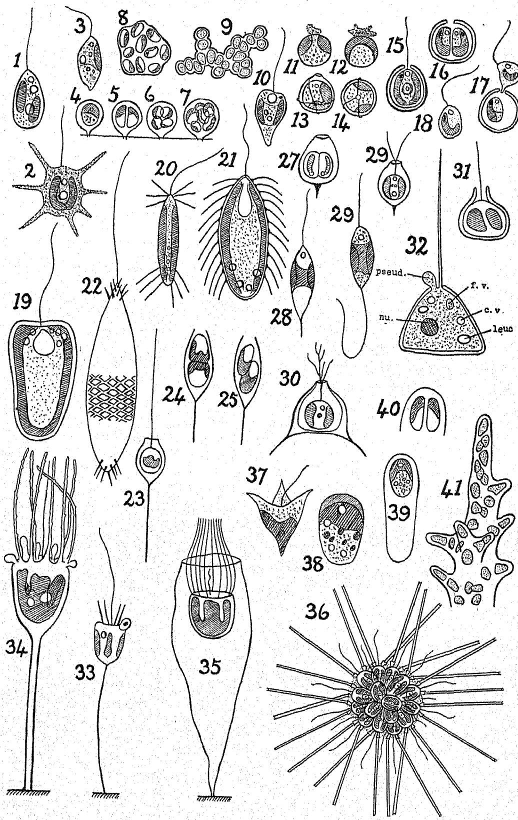


Fig. 5. CHROMULINALES.—1 and 2, *Chrysamœba radians* Klebs: 1, a normal free swimming individual; 2, an amœboid form. 3 to 9, *Chromulina Rosanoffii* (Woronin) Bütschli: 3, motile cell or zoogonidium; 4 to 7, division of a motionless encysted cell floating on the surface of the water; 8 and 9, formation of palmella stage. 10, *Chromulina ovalis* Klebs, motile cell. 11 to 14. *Chromulina nebulosa* Cienk., showing development of cyst: in 11 and 12, a portion

of the protoplasm is extruded from a pore, this amœboid mass being used up in the formation of the cyst membrane; 13 and 14 are different views of the fully formed cyst. 15 to 18, *Chrysococcus rufescens* Klebs: 15, a motile cell, in optical section, showing projection of the flagellum through a pore in the thick perisarc; 16, division of the protoplast; 17, escape of a daughter-cell; 18, free daughter-cell, before formation of perisarc. 19, *Microglena punctifera* Ehrb., showing the vacuole system. 20, *Mallomonas litomesa* Stokes, with flinty processes at anterior and posterior ends of the cell, 21, *Mallomonas acaroides* Ehrb., with similar processes nearly covering the cell. 22, *Mallomonas pulcherrima* Stokes, showing in part the reticulate sculpture of the perisarc. 23 to 25, *Stylococcus aureus* Chodat: two stages of division in 24 and 25. 26 to 30, *Chrysopyxis bipes* Stein: in 26 the flagellum is forked; 27 shows longitudinal division into two daughter-cells; 28 and 29, a daughter-cell with elongating posterior process for attachment—in 30 this process has wound around a *Zygnema* filament, part of which is seen in transverse section at the base of the sessile flask-like perisarc. 31, *Lagynion Scherffeli* Pascher. 32, *Heterolagynion Oedogonii* Pascher: to the left of the stout motionless flagellum is a short blunt pseudopodium *(pseud.)*; within the stout perisarc the protoplasm contains a nucleus *(nu.)*, a food vacuole *(f.v.)*, two contractile vacuoles *(c.v.)*, and two leucosin masses *(leuc.)* 33, *Pedinella hexacostata* Wys., with four stiff bristles at the base of the flagellum; on the right is an amœboid pseudopodium containing a food vacuole. 34, *Cyrtophora pedicellata* Pascher, showing the central flagellum, the stout nodulose tentacles, and several pseudopodial processes at the anterior end of the protoplast. 35, *Palatinella cyrtophora* Laut., with short flagellum in the centre of the ring of tentacles. 36, *Chrysosphærella longispina* Laut., a motile cœnobium of *Chromulina*-like cells, each with two long flinty processes exserted from cup-like outgrowths of the periplast. 37 to 41, *Hydrurus fœtidus* (Vauch.) Kirchner: 37, a motile cell or zoogonidium; 38, motionless cell, which becomes attached by a gelatinous stalk (39) and by division (39) gives rise to the branching colony, a portion of which is shown in 41.

1, 2, 10, 15 to 19, 21, 37 to 40, from Klebs; 3 to 9, from Woronin; 11 to 14, from Cienkowsky; 20, 22, from Stokes; 23 to 25, from Chodat; 26 to 30, from Stein; 31, 32, 34, from Pascher; 33, from Wysotzki; 35, 36, from Lauterborn; 41, from Berthold.

Hydrurus and other palmelloid Chrysomonads have been regarded by some writers as belonging to the Phæophyaceæ, on account of the dominance of the palmella stage in the life history, but apart from the fact that various degrees of elaboration of this stage have been observed in undoubted Flagellates, the terminal insertion of the flagella in the lower Chrysomonads, as compared with the characteristic lateral flagella of the Brown Algæ, seems to form an insuperable obstacle to the derivation of the Phæophyceæ from these Chrysomonads. Despite the dominance and elaboration of its palmella stage, *Hydrurus* can hardly be said to have crossed the "border-line" between Flagellates and Algæ; it is simply a Flagellate, allied closely to the lower Chrysomonads, and represents the culmination of a line of palmelloid forms arising from types like *Chrysapsis* and *Nannochrysis*. The "Volvocine tendency" shown in *Chromulina Hokeana* is carried further in *Chrysostephanosphæra*, recently discovered by Scherffel; here the cœnobium consists of sixteen cells arranged as in *Stephanosphæra* on the equator of a globular gelatinous mass, but later a palmelloid state is produced in which each cell has its own mucilaginous envelope.

Further elaboration in the external and internal characters of the cell is seen in the small family of Mallomonadaceæ, consisting of the two free-living genera *Mallomonas* and *Microglena* and the colonial genus *Chrysosphærella*. In *Mallomonas* (Fig. 5, *20-22*) the

ovoid or elongated cell has a close-fitting shell composed of tesselated polygonal plates, and either each plate, or only those at the two ends of the body, may bear fine silicified outgrowths; there are two chromatophores, and the hinder end of the cell contains numerous contratile vacuoles, while at the anterior end there is a large non-contractile vacuole; the cysts are also covered with a silicified shell. In *Microglena* (Fig. 5, *19*) the vacuole system is further elaborated, all the vacuoles being anterior, the smaller contractile vacuoles surrounding a large non-contractile vacuole; there is frequently a single basin-like chromatophore; the shell is thin and bears only scattered granular outgrowths. In *Chrysosphærella* (Fig. 5, *36*) the cells are united by their hinder ends in a spherical jelly, forming a motile *Pandorina*-like cœnobium; each cell bears on its free outer (anterior) end two small cup-like outgrowths from the shell (which has the same structure as in *Mallomonas*) and from each of these cups there springs a long flinty spicule; the internal structure of the cells resembles that of *Microglena*, there are two chromatophores, each with a stigma.

Pascher (102) has founded a fourth family of Chromulinales, the Cyrtophoraceæ, upon three very remarkable epiphytic genera which have probably arisen from a type like *Chrysopyxis*. These genera—*Pedinella*, *Palatinella*, *Cyrtophora* (Fig. 5, *33-35*)—are either sessile or stalked, the body is flattened anteriorly and bears a central flagellum surrounded by from six to twenty pseudopodia; there is a single basin-shaped chromatophore, but this is more or less deeply lobed in front. Pascher (109) has recently described a genus (*Lagynion*) which forms a transition between *Chrysopyxis* and the Crytophoraceæ; in *Lagynion* (Fig. 5, *31*) the cell is fixed by a broad base, and within the collar-like projecting portion of the shell the protoplast protrudes short amœboid pseudopodia around the base of the long motionless flagellum or "rhizopodium." The same writer describes a colourless genus, *Heterolagynion* (Fig. 5, *32*,) evidently derived from *Lagynion*, and points out that the Cyrtophoraceæ show a remarkable parallelism with the Pantostomatinean genera *Pteridomonas* and *Actinomonas*.

In the Isochrysidales the cells are either free-living or united to form colonies of the Volvocine type. Of the nine genera placed here (as Hymenomonadaceæ) by Senn, the unicellular genus *Wysotzkia* should be transferred to the Phæochrysidales (Cryptomonads), and the palmelloid genera *Phæocystis* (Ostenfeld 96), and *Nægeliella* (Correns, 27) to the Phæocapsaceæ; in these three genera the two flagella are inserted laterally, and while *Wysotzkia* is clearly related to the simpler Cryptomonads, especially to the two recently discovered genera *Protochrysis* and *Cryptochrysis*, it seems equally obvious that the affinities of *Phæocystis* and *Nægeliella* are with the lower Phæophyceæ, hence they should be removed from the Brown Flagellata altogether. In the simplest Isochrysid genus, *Hymenomonas* (Fig. 6, *1*), the cell has a firm thick periplast, though the anterior portion of the protoplast is naked and capable of putting forth pseudopodia. In this order, evolution appears to have taken place in two directions, one leading to epiphytic forms recalling *Chrysopyxis* and its allies among the Chromulinales, the other to motile colonies. Of the epiphytic forms, *Stylochrysalis* (Fig. 6, *3*),

is attached to its substratum (usually an *Eudorina* colony), by a long stalk dilated at the base, and has a thin periplast; while *Derepyxis* (Fig. 6, *2*) resembles *Chrysopyxis* in having an outstanding perisarc with a projecting collar. Of the colonial forms, *Syncrypta* and *Synura* have globose motile cœnobia, consisting of 16 to 64

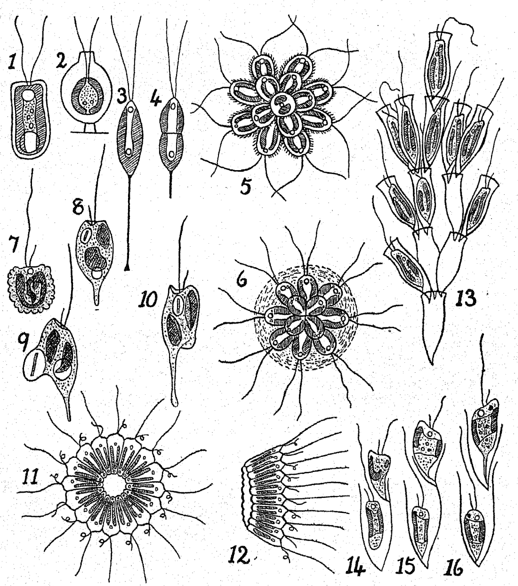


Fig. 6. Isochrysidales (1 to 6) and Ochromonadales (7 to 16).—1, *Hymenomonas roseola* Stein. 2, *Derepyxis dispar* Stokes. 3, *Stylochrysalis parasitica* Stein (in 4, transverse division is shown). 5, *Synura Uvella* Erhb. 6, *Syncrypta Volvox* Erhb. 7, *Ochromonas crenata* Klebs. 8 to 10, *Ochromonas mutabilis* Klebs, showing migration of food vacuoles within the protoplasm and amœboid changes of form of the cell. 11, 12, *Cyclonexis annularis* Stokes: in 11 the cœnobium is seen from the surface, in 12 from the side. 13 to 16, *Dinobryon Sertularia* Ehrb.: in 14 to 16, stages in division and perisarc formation.

1, from Klebs; 2, 11, 12, from Stokes; 3 to 6, from Stein; 7 to 10, 14 to 16, from Klebs; 13, from Senn.

biflagellate individuals closely aggregated in a radial manner, their pointed hinder ends directed towards the centre of the cœnobium; in *Syncrypta* (Fig. 6, *6*) the cells have a thin periplast and the

colony is invested in mucilage through which the flagella protrude, in *Synura* (Fig. 6, *5*) there is no mucilaginous covering and each cell of the colony has a firm periplast beset with spines or warty outgrowths—in *S. Klebsiana* each cell bears two flinty spicules, as in *Chrysosphærella*. Pascher (110) has observed that in *Synura uvella* the contents of a cell may escape as an amœba instead of a flagellate swarmer, and that the latter may also become amœboid after liberation, and that from both flagellate and amœboid forms palmella-states may arise by division in a mucilaginous motionless condition (Conrad, 26).

The Ochromonadales, though a smaller order than the Chromulinales and Isochrysidales, shows parallel developments of the same kind. Here again we begin with a unicellular and potentially amœboid type, *Ochromonas* (Fig. 6, *7-10*), which, except in having two unequal flagella, closely resembles *Chrysamœba* among the Chromulinales; most of the species are free-swimming, but *O. tenera* becomes fixed by its hinder end; the thin periplast is capable of secreting mucilage, and in *O. socia* division occurs in the motile phase and gives rise to small, generally four-celled, motile cœnobia; usually, division occurs in a resting state, and in *O. botrys* a large mass of cells enveloped in mucilage may be formed in this way. In *Cyclonexis* (Fig. 6, *11, 12*), the individual cells are like those of *Ochromonas*, but they remain in lateral contact in such a manner as to form a radiating ring-like cœnobium, consisting usually of 16 cells. In *Uroglena* a curious type of cœnobium is formed as the result of repeated division of the stalked cells and the formation of a spherical mucilage mass in which the cells lie near the periphery while the branching stalks radiate from the centre. In *Dinobryon* (Fig. 6, *13-16*) the cell is spindle-shaped and is invested loosely by a vase-like shell widely open above; when division occurs, the daughter cells may either escape or (in most species) become attached to the mouth of the shell and produce a shell of their own; by repetition of this process, a branching colony is built up; the shell in some cases gives cellulose reactions. The genus *Dinobryon* has been monographed by Brunnthaler (16) and by Lemmermann (79).

VII.—The Cryptomonads and their Relationships.

It would appear that the three orders of Chrysomonadineæ dealt with thus far (Chromulinales, Isochrysidales, Ochromonadales) have not given rise to anything higher than a Flagellate, though they show various attempts at the formation of colonies —in all three orders we find gradual elaboration of motile "Volvocine" cœnobia, and also the working out of a palmelloid or "Tetrasporine" tendency towards the formation and dominance of a non-motile multicellular vegetative condition. It may be noted that "Volvocine" cœnobia occur also among the Protomastigineæ (*Protospongia*, *Sphæræca*, etc.), in addition to the dendroid colonies of the *Dinobryon* type (*Codonocladium*, *Salpingœca*, etc.) derived from solitary "choanflagellate" forms (*i.e.*, forms with outstanding collar-bearing perisarc). Whether the remarkable resemblances between the "mastigamœboid," the "Volvo-

cine," and the solitary and dendroid "choanoflagellate" types met with in the colourless Pantostomatineæ and Protomastigineæ on one hand and the Chrysomonadineæ on the other are to be interpreted as examples of parallel developments, or whether, as suggested by Pascher and Scherffel, they indicate derivation of part at any rate of the colourless Flagellate families from Chrysomonads, the trend of recent work on the Brown Flagellata is decidedly against the view that the Chrysomonads comprised in families Chromulinales, Isochrysidales, and Ochromonadales have given rise to the Brown Algæ.

The case appears to be quite different with the fourth Chrysomonad order, the Phæochrysidales or Cryptomonads, which are distinguished by the *lateral* insertion of the two flagella. The simplest forms are Pascher's new genera *Cryptochrysis* and *Protochrysis* (103); *Wysotzkia* (hitherto placed in the Isochrysidales); and *Nephroselmis* (Senn, 136), which Wille (150) includes in the Volvocaceæ. Senn (135) defines the Cryptomonads as having an ovoid and flattened body, with two equal flagella arising just behind the anterior end from a groove which is continued into a gullet-like cavity, and having one or two contractile vacuoles which are not coördinated into a pulsating system. According to Senn they are also further differentiated from the Chrysomonads by producing starch, or, at any rate, a refractive solid carbohydrate. The researches of Pascher and others have shown, however, that the Cryptomonads, though a highly specialised group, cannot be set apart from the Chrysomonads, as a separate group of the Flagellata, and that they have arisen from the Chrysomonads by further internal differention of the protoplast, accompanied by a shifting of the flagella from a terminal to a lateral position. In *Wysotzkia* (Fig. 7, *3*, *4*), the posterior end of the protoplast, behind the two chromatophores, is naked and capable of amœboid movement. In *Cryptochrysis* (Fig. 7, *2*), the lateral insertion of the flagella is more marked than in *Wysotzkia*, the flagella arising from a deep longitudinal groove which is about half the length of the body and is covered with minute granules; nutrition is purely holophytic and the assimilate consists of disc-like grains giving a reddish violet colour with iodine; division takes place in the motile state, and is longitudinal.

Cryptochrysis appears to be the most primitive Cryptomonad at present known; *Wysotzkia*, though simpler in some respects, undergoes transverse division, and is adapted for partial or facultative holozoic nutrition. *Nephroselmis* and *Protochrysis* differ from these genera, and indeed from the remaining Cryptomonads, in that the groove is transverse and occupies the middle of the protoplast, so that the flagella arise from the middle of the concave side of the body; in *Nephroselmis* there is a single chromatophore which follows the outline of the body and is interrupted only at the point of emergence of the flagella, and division occurs in the motile condition, whereas in *Protochrysis* (Fig. 7, *1*), there are two chromatophores, and division occurs after the cells have become rounded off and invested in mucilage, a four- or eight-celled colony being formed by repeated division in this palmella-state. In *Cryptomonas* (Fig. 7, *5*—*7*), the groove found in the

genera just mentioned is replaced by a canal which leads into the interior of the protoplast; in some species this canal is quite short, in others it extends for about half the length of the body. In most species of *Cryptomonas* the assimilate is like that found in *Crypto-*

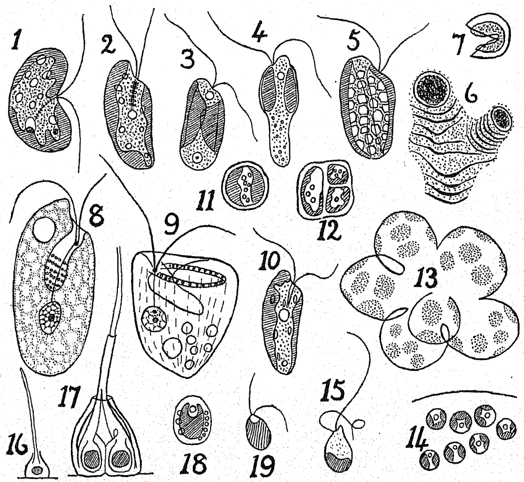


Fig. 7. CRYPTOMONADS (1 to 9) and PHÆOCAPSACEÆ (10 to 19):— 1, *Protochrysis phæophycearum* Pascher. 2, *Cryptochrysis commutata* Pascher. 3, 4, *Wysotzkia biciliata* (Wys.) Lemmerm.: 3, ordinary form; 4, metabolic (amœboid) form, showing protrusion of pseudopodia anteriorly and posteriorly. 5 to 7, *Cryptomonas erosa* Ehrb.: 5, ordinary motile cell; 6, two encysted cells with gelatinous envelopes; 7, ruptured cyst membrane. 8, *Chilomonas Paramæcium* Ehrb.: the flagella arise on the ventral side of the "gullet" (which shows several circles of granular markings in its lower half), from a small body which is connected with the nucleus by means of a long fibril. 9, *Cyathomonas truncata* (From.) Fresen.: structure essentially as in *Chilomonas*; there are numerous food vacuoles at the base of the cell, the single contractile vacuole is seen near the opening of the "gullet." 10 to 12, *Phæoplax marina* (Reinisch) Pascher: 10, motile cell; 11 and 12, young colonies (beginning of palmella stage, which when fully developed resembles that seen in *Chromulina Rosanoffii*, Fig. 5, 9). 13 to 15, *Phæocystis Poucheti* Lagerh.: 13, gelatious colony (palmella state); 14, a portion of same, more highly magnified); 15, a motile cell (zoogonidium). 16 to 19, *Nægeliella flagellifera* Correns: 11 and 12, one-celled and three-celled stages in development of colony, showing the perisarc and bristles; 18, a single cell, showing the bell-shaped chromatophores; 19 a motile cell (zoogonidium).

1, 2, from Pascher; 3, 4, from Wysotzki; 5 to 7, from Senn; 8, 9, from Ulehla (with some details inserted from Hartmann and Chagos); 10 to 12, from Reinisch; 13, 14, from Lagerheim; 15, from Pouchet; 16 to 19, from Correns.

chrysis, but in *C. ovata* starch is produced; longitudinal division may occur in either the motile or the encysted condition, and the cyst membrane gives the reactions of the cellulose. *Chroomonas* and *Cyanomonas* resemble *Cryptomonas*, but the chromatophores are blue-green, while *Rhodomonas* is allied to these forms but has a red chromatophore. *Chilomonas* (Fig. 7, *8*) also resembles *Cryptomonas* in structure, but is saprophytic, though it produces starch; *Botryomonas* (Schmidle, 131) is another saprophytic starch-producing form, in which the cells become aggregated to build up a branched gelatinous colony, and the periplast gives cellulose reactions. *Cythomonas* (Ulehla, 143) and *Oxyrrhis* (Senn, 136), though placed by Senn in the Protomastigineæ, are apparently related closely to *Cryptomonas* through *Chilomonas*, and may be regarded as colourless forms derived from a *Cryptomonas*-like type; in *Cyathomonas* (Fig. 7, *9*) nutrition is mainly saprophytic, but solid food can also be ingested at the anterior end of the body, while in *Oxyrrhis* nutrition is mainly holozoic and this genus differs from its allies in undergoing transverse division.

The Cryptomonads have probably arisen from simple Chrysomonads, with two flagella either of unequal length or with different orientation (one directed forwards and the other backwards in swimming). Such a form as *Ochromonas*, for instance, may well have given rise to the Chloromonadineæ on one hand and to the Cryptomonads on the other, for these two groups show somewhat striking parallelisms, such as the organisation of the vacuole system into small actively contractile vacuoles which open into a large anterior non-contractile vacuole or into a groove or canal. The Chloromonads have probably given rise on one hand to the highly differentiated Eugleninеæ which have no Algal affinities, and on the other to the Algal group "Confervales" (Heterokontæ). Similarly the simpler Cryptomonads—e.g., *Cryptochrysis* and *Protochrysis*—appear to have given rise on one hand to highly organised Flagellates like *Cryptomonas*, *Chilomonas*, *Cyathomonas*, and *Oxyrrhis*—corresponding to the Eugleninеæ in the green series—and on the other to the Phæocapsaceæ, which form the starting-point of the Brown Algæ.

The Phæocapsaceæ, corresponding roughly with the Tetrasporaceæ and Palmellaceæ in the green series, are apparently a somewhat heterogenous group, marked by the dominance of the non-motile phase. One of the simplest genera is *Phæocystis* (Fig. 7, *13-15*) in which the cells have from one to four plate-like chromatophores and are aggregated to form a rounded gelatinous colony, the motionless cells being rounded, while the motile cells ("zoogonidia") are biflagellate and have the same structure as *Wysotzkia* (Lagerheim, 73; Ostenfeld, 96; Scherffel, 122). In a similar form described by Reinisch (120) as *Phæococcus marinus* (Fig. 7, *10-12*) but regarded by Pascher (104) as the type of a new genus, *Phæoplax*, the motile cells correspond closely to *Cryptochrysis*. *Phæococcus Clementi* is a gelatinous form adapted to subaërial life, the cells having firm envelopes, and the motile cells show typical Cryptomonad structure; whether *P. paludosa* described by West (146) belongs to this genus, or indeed to the Phæocapsaceæ, is somewhat doubtful, since in his figures the motile cells resemble those of the Isochrysidal Chrysomonads and not the Cryptomonads.

The position of *Phæosphæra* West is also doubtful, as the motile cells have apparently not yet been observed; the same is the case with *Stichoglœa* and *Gleothamnion*, which would be included in the Phæocapsaceæ if their motile cells were found to show Cryptomonad characters. *Nægeliella* is epiphytic and forms multicellular discs, the individual cells producing a perisarc prolonged into a bristle; the motile cells have a single brown chromatophore and two laterally inserted flagella. The genus *Phæothamnion* appears to represent the highest form of the Phæocapsaceæ, while *Pleurocladia* leads directly to the Ectocarpaceæ and is placed in that group by Kjellman and Svedelius (66). A useful bibliography of the genus *Phæothamnion* is given by M'Keever (91), who recently discovered *P. confervicolum* (the only species known) in Scotland—it was previously recorded only from Sweden, Germany and Italy. There appears to be some doubt as to the insertion of the flagella and the nature of the motile cells; according to Lagerheim the latter are zoogonidia with terminal flagella and no eye-spot, while Borzi described the conjugation of isogamous gametes with lateral flagella and a red stigma. Oltmanns (95) places *Phæothamnion*, with the other genera here regarded as forming the family Phæocapsaceæ, among the Chrysomonadineæ. This genus is, however, apparently related very closely to *Pleurocladia*, which has the typical gonidangia and gametangia of the Ectocarpaceæ. Bohlin's genus *Phæodactylon* (9) cannot be included in the Phæocapsaceæ, but is probably a Chrysomonad in which adaptation to plankton conditions has resulted in loss of the flagella; its curious three-armed cell recalls the tetrahedal motile cells of *Hydrurus*.

The greatest difficulty in the way of deriving the Phæophyceæ from the Brown Flagellates has been the characteristic lateral insertion of the flagella in the motile cells of the Brown Algæ—excepting in the Dictyotaceæ, which are somewhat isolated among the Phæophyceaæ. This difficulty has, however, been overcome by the discovery of *Protochrysis*, in which the furrow from which the flagella arise, instead of being longitudinal and subapical as in other Cryptomonads, is transverse, so that the flagella arise from the middle of the body, one flagellum being directed forwards and the other backwards. *Protochrysis* appears to stand very near the ancestral type which gave rise to the lower Phæophyceæ or to the series of transitional forms (Phæocapsaceæ) leading through *Phaeothamnion* and *Pleurocladia* to the Ectocarpaceæ.

The work of Pascher and Scherffel supports Klebs' view that the Cryptomonads have arisen from the Chrysomonads and have no direct relationships with any other Flagellate group excepting possibly the Dinoflagellata (Peridiniales). Pascher, as we have already seen, merges the Cryptomonads in the order Chrysomonadineæ, and has shown that the organisation of a pulsating vacuole system, previously regarded as found only in the Chloromonads and the Eugleninéæ, occurs not only in the Cryptomonads but also among the Chrysomonad groups. Another distinction made by previous writers between the Cryptomonads and Chrysomonads has broken down, namely, that relating to the nature of the assimilation products. According to Senn, the Chrysomonads produce oil and leucosin, and nutrition may be holozoic or saprophytic or holophytic, while in the Cryptomonads starch is produced and nutrition is

never holozoic. Pascher has shown, however, that although starch is formed in certain Cryptomonads (*Cryptomonas erosa, Chroomonas baltica, Chrysidella, Chilomonas*), this is not the case in other forms which have been investigated (*Protochrysis, Cryptochrysis, Chroomonas Nordstedtii*) nor in the Phæocapascæ, where the assimilate is either leucosin or oil. All that can be said on this head is that solid assimilation products are relatively rare in the Chrysomonads and relatively common in the Cryptomonads. Again, the beginnings of the characteristic furrow of the Cryptomonads are seen in the Ochromonadales, and even in the Chromulinales, where the anterior end of the body shows a pit in which the flagellum is inserted.

(*To be continued*).

LABORATORY NOTES.

METHOD OF DOUBLE-STAINING MICROTOMED SECTIONS IN THE RIBBON.

In the course of an investigation on the anatomy of the rhizome of *Statice Limonium*, considerable difficulty was experienced owing to the fact that though the tissues embedded well in paraffin, and cut easily, immersion in xylol for the removal of the wax immediately washed the sections from the slide This was probably due to the fact that the periphery of the sections is occupied by a well developed cork layer which adheres imperfectly to the slide (although the egg-albumen was known to be in good condition), and tends to separate from it even during the drying process following on the floating-out of the ribbon in water. As it was necessary to obtain serial sections, various experiments were tried based on the methods described by T. G. Hill,[1] and the following are the chief results obtained.

METHOD I. *Sections which show a tendency to wash off the slide.* e.g., *Statice Limonium* rhizome.

The ribbon is floated out on the prepared slip with Delafield's Haematoxylin,[2] the slip is warmed until the sections are quite flat and the superfluous stain is then drained back into the bottle. The Hæmatoxylin is replaced by a saturated solution of Safranin in 50% alcohol, care being taken that the stain flows under the ribbon and not over it; after a few minutes the stain is drained off, the sections are "blotted down" with hard smooth blotting paper, and the slide is allowed to dry either by exposure to air or by warming. The preparation is completed, *without removal of the paraffin*, by mounting in rather liquid canada balsam.

If a single stain is sufficient, either Safranin or Gentian Violet gives excellent results, since the tissues are stained generally.

1. A method of Staining Microtomed Sections in the Ribbon. New Phyt. Vol. xi, No. 2, Feb. 1912.

2. Ehrlich's Hæmatoxylin gives very poor results, and Mr. Hill informed me that this was the formula he used.

It might be supposed that mounting in the paraffin in this way would tend to obscure the tissues through the staining of the paraffin itself. If, however, the excess of stain is drained off thoroughly and the sections gently pressed down with blotting paper, very clean preparations are obtained, the wax being stained hardly appreciably. If the slides are warmed after mounting, the rather liquid canada balsam (in xylol) dissolves the wax almost entirely, if not quite.

If the sections do not shew a tendency to wash off the slide, the following method is preferable.

METHOD II. *Sections which adhere to the slide and do not wash off.*

The process described under Method I is followed as far as the "blotting down" of the ribbon. The slide is then gently warmed until the paraffin has melted and the wax is removed by treatment with xylol. If necessary the staining can be controlled at this stage by rinsing in absolute alcohol; clearing with xylol follows and the preparation is completed by mounting in canada balsam.

Equally good results are obtained in Method II by mixing the Hæmatoxylin and Safranin (equal parts) and floating the ribbon on the mixture, for any overstaining can be controlled by washing in absolute alcohol after removal of the wax.

Various other stains have been tried, with the following results:

1. A saturated solution of Safranin in 50% alcohol, followed by a satsrated solution of Lichtgrün in clove oil gives exceptionally good preparations for details of structure. For example, in a transverse section of the root of *Cephalotaxus* stained in this way, the thickenings on the walls of the *assise de soutien* are stained red, the cell-walls greenish red, and the protoplasmic lining to the cells bright green.

2. An alcoholic solution of Safranin followed by Methyl Green gives fairly good differentiation.

3. Methyl Green followed by Delafield's Hæmatoxylin is less satisfactory.

4. Gentian Violet followed by either Bismark Brown or Vesuvian Brown gives poor results.

The preparations made by these methods are quite as good as those obtained by the means commonly employed in double-staining processes. The methods have the great advantage that the whole process of double-staining and mounting a slide can be carried out in from 5 to 10 minutes hence the time-factor, which becomes of such importance in investigation, involving the anatomical examination of much material, becomes very considerably lessened by the double-staining of microtomed sections in the ribbon.

E. DE FRAINE.

UNIVERSITY COLLEGE, LONDON,
February 13th, 1913.

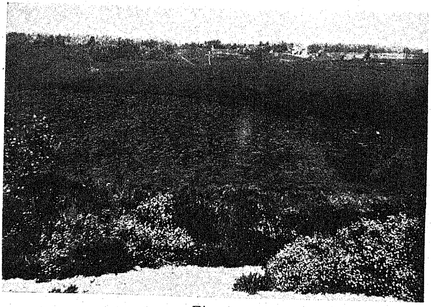


Fig. 1.

Fig. 2.

Fig. 3.

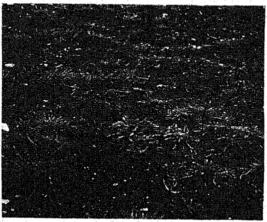


Fig. 4.

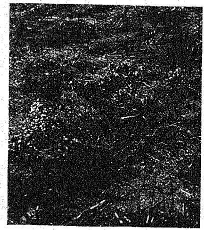


Fig. 5.

FRITSCH AND PARKER—HEATH ASSOCIATION, HINDHEAD.

THE

NEW PHYTOLOGIST.

VOL. XII, NOS. 4 & 5. APRIL & MAY, 1913.

[PUBLISHED MAY 29TH, 1913].

THE COEFFICENT OF HUMIDITY: A NEW METHOD OF EXPRESSING THE SOIL MOISTURE.

BY W. B. CRUMP, M.A.,

Heath Grammar School, Halifax.

[WITH ONE FIGURE IN THE TEXT.]

I.—INTRODUCTION.

THE most obvious distinction between plant habitats is that based upon the quantity of water present and the permanence or fluctuation of the water supply. Such common descriptive terms as marsh, swamp, desert, or wet, boggy, dry, express this and serve to differentiate habitats in a general way. Proceeding further by deduction, field botanists are accustomed to estimate the comparative wetness of an area by the vegetation it supports, or by the presence of specific plants. But the development of ecology demands the replacement of these indefinite characters by more exact knowledge based upon quantitative analysis of the edaphic factors; knowledge of the magnitude of each that produces the static equilibrium revealed as a stable plant-association, and of the limiting values that determine the dynamic change from one association to another, or even the replacement of one formation by another. At present the nature of the master-factors that determine the existence of a formation is often a matter of supposition. Until a body of *data* has been accumulated it is impossible to know which of several possible factors controls the formation, or what is the magnitude of a given factor when it reaches its limiting value.

The importance of quantitative determinations of water-contents has been insisted on by F. E. Clements[1] and in laying stress on the water-content, and particularly the available water-content or chresard, as of more importance than the soil structure

[1] "Research Methods in Ecology." Lincoln (Nebraska), 1905.

he has indicated a promising field for research in Ecology. But very little progress has been made in opening it out and this, apparently for two reasons. The direct determination of the available water-content in the field is impracticable under ordinary conditions, and when attempts have been made to determine the total water-content—the actual amount present as distinct from the maximum when the soil is saturated—the results have been discordant or inconclusive. So it comes about that whilst much attention has been given to soil physics and the relation between soil structure and water capacity, the particular information desired by the ecologist—the actual amount of water within the zone of root activities—is still non-existent. But the need of it is urgent. Even when definite soil types have been distinguished according to their chemical nature and physical structure and when the natural vegetation has been correlated with these types, the investigation is at least incomplete. To leave the water-content out of consideration is to omit the factor which links the two, the soil and the plant, together. Granted that the soil structure controls the water-content, still the latter may prove a much better index of the plant environment, either because it can be determined more simply, or expressed with greater precision, or because its relation to the plant is more direct and intimate. There may be cases where the nature of the soil is the controlling factor, but so long as the water-content is unknown its influence can neither be predicated nor denied.

But it is necessary to consider at the outset whether it is possible to obtain a value for the water-content that will be in any way expressive of the habitat. Can it be regarded as a constant whose value for any given association may be determined by a series of analyses? How are the irregular fluctuations and the seasonal variation in the quantity of water present in the soil to b eliminated? Is it the mean value, or the maximum in the we season, or the minimum in the dry season, that is the mor significant? Is the range within such bounds as to afford . mean value that is in any way a criterion of the habitat? Experi mental results afford an answer to such questions and soon sho that the investigation of a plant-habitat does not admit of th rigorous measurement applicable in physics and chemistry. I the water-content of the *Calluna* habitat, for example, is constant of nature it differs radically from an atomic weight a can never be stated with the same exactitude, for it is of necess subject to considerable variation.

But variation from a specific type is axiomatic in biology and the determination of the mean or "mode" corresponding to the type has become a familiar problem in biometrics. Such a point of view is necessary in dealing with soils as plant-habitats. The number of veins in a beech leaf, as shown by Karl Pearson,[1] varies considerably, but by examining a large number of leaves a type, represented by the mode, can be established and the greatest number of individuals is aggregated round this mode. Beech leaves from another locality will possess an appreciably different mode and the range of variation will be extended by increasing the number of observations. But the extreme deviations from the mode will occur very rarely, in accordance with Galton's Law of Frequency.

Whether or no the water-content is the best method of expressing the soil-moisture may be left in abeyance for the moment. Whatever is selected as the criterion of the humidity of the habitat its values will show variation about a mean. If the deviations follow the normal curve of frequency, supposing a sufficient number of observations to have been made, the mean affords a definite index of the habitat, and a habitat that satisfies such a test is as much an entity as is a biological species. The extreme deviations will possess considerable significance, for they will indicate the physiological limits of the existence of the plant association. Above and below these limits the association can no longer exist and even before these points are reached it is likely to be invaded by members of other associations. Of the two, the minimum value probably has the greater significance for ecological purposes. If it is determined under such conditions as prevailed during the summer of 1911 it must give a close approximation to the true value of Clements' echard, or the non-available water in the soil, perhaps more so than values obtained "under control," or by cutting out blocks in the field.

II.—Method of Analysis.

Before proceeding to explain the method adopted for expressing the soil-moisture it is necessary to review briefly the process of analysis and the reduction of the results.

The soil sample taken within the layer of root activity is preserved in a tight tin. If in the laboratory it does not appear to be uniform it is divided into an upper and a lower layer and suitable blocks from the centre of each are rapidly weighed in tared porcelain dishes, after larger rootlets have been removed if present. These

[1] The Grammar of Science.

samples weigh from 15 to 60 grams, and the weight is determined within a centigram. They are then placed in a quiet room or airy cupboard and left to dry at about 15°C. until the weight is constant. This takes from one to three months. The loss of weight is the required water-content. The dishes are then heated in a water-oven (at 100°C.) until the weight is again practically constant. This further loss at 100°C. though recorded is *ignored* because it can be of no service to the plant. It includes hygroscopic moisture and water of combination and its value is tolerably uniform for the same type of soil so that it affords a check on the determination of the water lost at 15°C.

The dish and its contents are next subjected to a full red heat until all char has disappeared, and again weighed as soon as cold, or preferably placed in a desiccator to cool. The loss of weight is recorded as humus, as a more definite term than "loss on combustion" and quite in accordance with the use of the word humus to include all the decaying organic matter in the soil. The residue may consist entirely of vegetable ash, or may be almost wholly mineral in origin. If the soil is calcareous the lime must be reconverted into carbonate after combustion.

Such is the process of analysis. The percentage composition of the *wet* soil is then calculated from the results. But partly to conform to agricultural practice and partly because the wet soil represents no fixed standard, the values are then manipulated to express them in terms of 100 parts of *air-dry* soil, *i.e.*, of soil dried at 15°C. The water-content, otherwise the loss at 15°C., then becomes an *addition* to the 100 parts. Clearly, if a wet peat loses just 50% of its weight on drying in the air, the air-dry peat was "combined with" 100% of water. The principle is sound though it has dis-advantages, for when the water-content is high originally it b[illegible]ecomes much exaggerated in the final result. Even if agricultura[illegible] analyses took note of the water lost on drying at 15°C. this di[illegible]advantage would not be apparent. But in the case of peats th[illegible] statement of the water-content is paradoxical unless the exact [illegible] expression receives careful attention, *e.g.*, "the water lost at 15°C [illegible] 135% of the air-dry peat," means that there are 135 parts of [illegible] water lost on every 100 parts of the air-dry peat that re[illegible] after drying. Slight differences are of cour[illegible] same way, so that a variation of 1% in the [illegible] peat may become 50% in terms of the ai[illegible] The rapi[illegible] increase in the higher terms is shown in the following table:—

Water-Content.

In terms of wet soil.	In terms of air-dry soil.
10%	12·5%
25	33·3
50	100
70	233·3
80	400
85	566·6

All values quoted in the paper are expressed in terms of the air-dry soil.

III.—Variability of the Water-Content.

So far the water-content has been assumed to be the only measure of the soil-moisture, as in fact it has hitherto been regarded. But it has already been implied that it proves to be a very imperfect index of the soil conditions, not because it varies, for the soil moisture is itself subject to variation, but because it varies irregularly and independently of the humidity of the soil. Broadly, the water-content will by its magnitude suffice to distinguish habitats if the soil is uniform to some depth, but that condition is rarely satisfied in natural habitats and can never be postulated. Still, there is no difficulty in differentiating a heather moor and a cotton-grass moor by the mean water-content of the peat, but in the majority of cases the evidence it affords is inconclusive or contradictory. Even on a heather moor, peat containing only 70 or 80% of water can be shown to be in reality wetter than peat containing 100 or 130% of water.

But the real difficulty in the use of the water-content is met with as soon as the section sampled is not of the same nature at successive depths. Where soils are shallow, as where peat overlies a coarse sand that rapidly passes into rock, or where a woodland humus covers a soil almost free from humus, the active rootlets may occupy both layers indifferently, though, as shown by Woodhead[1] and others, in certain cases these several layers are occupied by distinct members of the association. It was soon discovered that in analyses of such shallow soils the water-content diminished so rapidly at the boundary between the layers that the values were in no wise comparable, in spite of the fact that both related to the same plant. A few illustrations selected from and typical of the earlier stage of this investigation will make the point clear.

[1] "Ecology of Woodland Plants in the Neighbourhood of Huddersfield." Journ. Linn. Soc. Bot., Vol. XXXVII., p. 333.

Soil No. 13 (September, 1905). *Vaccinium Myrtillus* and *Deschampsia flexuosa* growing in a shallow hollow on a *Calluna* Moor, Yorks.

	Air-dry Peat. Water at 15°C.	Humus.	$\frac{\text{Water}}{\text{Humus.}}$
i. Loose fibrous peat $\frac{1}{2}$-$\frac{3}{4}$ ins.	176·4%	78·8%	2·23
ii. Compact peat $\frac{1}{4}$-$\frac{3}{4}$ ins. ...	61·0	17·4	3·52
iii. Sandy "sub-peat" 1-2 ins.	21·1	8·1	2·59

Rootlets penetrating ii. and entering iii.

Soil No. 34 (March, 1906). *Vaccinium Myrtillus* and *Deschampsia flexuosa* in Oak Wood (*Q. sessiliflora*), Yorks.

	Air-dry Peat. Water at 15°C.	Humus.	$\frac{\text{Water}}{\text{Humus.}}$
i. Humus at 1-2$\frac{1}{2}$-ins. ...	170·0%	55·5%	3·06
ii. Sandy soil below i. ...	30·4	10·4	2·92

Rootlets permeating i. and extending into ii.

Soil No. 66 (September, 1906). *Nardus stricta* on *Nardus* pasture, Yorks.

	Air-dry Peat. Water at 15°C.	Humus.	$\frac{\text{Water}}{\text{Humus.}}$
i. Black soil at $\frac{1}{2}$-1$\frac{1}{2}$ ins. ...	67·4%	33·4%	2·01
ii. Same at 1$\frac{1}{2}$-2$\frac{1}{4}$ ins. ...	40·3	18·6	2·16

IV.—Water-Content a Function of the Humus-Content.

In the first two soils it is clear that no significant result can be obtained by averaging such divergent values for the water-content as are revealed by the analyses. The cause for the divergence is not far to seek: it is found in the varying quantity of humus present in the different layers. If then the humus is the disturbing factor, it seems probable that if its influence can be eliminated the successive layers will not prove very different, and the real humidity—the state of wetness—of the habitat can be assessed. This is done by reducing the humus to unity in all cases. In other words the water-content is expressed in terms of the humus-content, and the ratio $\frac{\text{water-content}}{\text{humus-content}}$ which is used as the new index of the soil moisture may be fittingly called the *coefficient of soil humidity*.

The importance of humus in increasing the water capacity of a soil has long been recognized. But the working hypothesis now formulated, is that the humus, as a colloid holds all, or practically all, the water in a humous soil, so that even with relatively small humus-contents the water holding power of the non-colloid consti-

tuents may be neglected. Leaving on one side the possibility that in other types of soil colloid clay may have a similar function, it remains to see how far the formula *the water-content is a function of the humus-content* provides in the coefficient of humidity a satisfactory instrument for gauging the soil moisture of a plant habitat.

Turning to the examples given above it is seen that in Nos. 34 and 66 the values of the coefficient in the two layers are practically identical. The natural interpretation of this is (1) that the humus is the sole cause for the difference in water-content; (2) that both layers are equally humid, in the same sense that the atmosphere may be equally humid on two days when the actual "water-content" is widely different. Its absolute magnitude is determined in the one case by the temperature of the air, in the other by the humus of the soil. So the coefficient measures the relative humidity of the soil, whilst the water-content measures its absolute humidity.

In No. 13 the coefficient values are not quite so consistent, but the case is partly chosen for that reason. The uppermost layer, above the roots, in spite of its high water-content has the lowest coefficient, which thereby reveals the superficial drying of the peat during the summer—a fact that could not be demonstrated in any other way. It is also noteworthy that the two habitats represented by Nos. 13 and 34, occupied by the same plants, exhibit very similar edaphic conditions.

Before turning to other examples in confirmation of these conclusions it may be as well to look at another possible explanation of the varying water-content in these soils. It may be argued that we have here merely a variable holard, or total water-content, of no physiological importance and that in spite of this variation the chresard or available water-content may be the same throughout, *viz.*, 20% or thereabouts. This implies a high echard (non-available water-content) in the case of peat, which in itself is not unreasonable, as there are other grounds for considering that bog plants (bog xerophytes) have difficulty in taking up water from wet peat. But this view appears untenable. There is no evidence that as a peat dries out until the wilting point is reached there is any change in the equilibrium between it and the sub-peat as regards the humidity. The evidence all goes to show that drying proceeds *pari passu* in peat and sub-peat. When each has lost all its physiological water, the echard, it is true is considerably higher in the peat than in the sub-peat, but the water is still distributed between the two according to the humus-content of each. The coefficient of humidity is lower

than before and has attained its wilting value, but it is still approximately the same for both.

Some wilting experiments on moorland plants[1] carried out in 1910 support this conclusion. On comparing the results obtained in the most extreme soils examined the differences lie within the experimental errors.

Wilting of *Eriophorum angustifolium*.

	Air-dry Peat. Water remaining (Echard).	Humus.	Water. / Humus.
Average of four cases	55·2%	71·1%	0·77
" " "	43·7	50·7	0·86

Wilting of *Calluna vulgaris*.

	Air-dry Soil. Water remaining (Echard).	Humus.	Water. / Humus.
Peat: average of three cases	25·9%	57·1%	0·45
Loam, or sand, ditto	3·0	7·6	0·36

Comparing these with the average coefficients of their natural habitats the inference appears to be that at the wilting-point the coefficients have about one-sixth their normal value. So five-sixths of the total water-content, irrespective of its amount, may be set down as physiological or available water.

V.—The Coefficient of Soil Humidity.

Now that the coefficient of humidity holds out the promise of being a standard index of the soil moisture, it becomes necessary to submit it to as wide a range of tests as possible to ascertain whether its values are sufficiently constant and distinctive to characterise both allied and diverse habitats—plant societies within an association as well as diverse formations.

Seasonal Variation. Many habitats show a sufficiently marked seasonal variation in the soil moisture to be reflected in the coefficient, as is shown in subsequent examples. But unless the seasonal variation is itself the subject of enquiry it seems better to limit the observations to the period of growth, which coincides roughly with the dry (*i.e*,, dry soil) season, between April and September. In no case should samples be taken within a few days of heavy rain and with this proviso, the results are reasonably comparable throughout the season. The ideal time to take samples

[1] Crump, W. B. "The Wilting of Moorland Plants." Report of the British Association, Portsmouth Meeting, 1911.

is towards the end of a two or three weeks' drought, and this can often be done in April, or June, or onwards to September.

Local Soil Variation. Samples to all appearance identical either from the same section, or from adjacent spots always show some, and often considerable variation in water-content. These accidental errors are entirely eliminated by the use of the coefficient of humidity. With this point in view the following samples of woodland soils, each to all appearance uniform, were divided and analysed separately. Their uniformity is confirmed by the results. Frequently when the samples are not as carefully chosen there is a more marked disparity in the water-content.

Ground Societies in Oak Wood on Coal Measures, Yorks., February, 1912.

			Air-dry Soil.		Water.
No.	Society.		Water at 15°	Humus.	Humus.
193.	*Scilla non-scripta*	(α) ...	24·4%	6·9%	3·5
		(β) ...	30·5	9·3	3·25
194.	*Carex pendula*	(α) ...	281·2	30·3	9·3
		(β) ...	248·3	26·7	9·28
195.	*Spiræa Ulmaria*	(α) ...	92·3	23·1	4·0
		(β) ...	90·0	22·0	4·08
197.	*Holcus mollis*	(α) ...	31·2	12·9	2·4
		(β) ...	28·6	12·1	2·36

The Moor Formation. A brief statement is all that is necessary, as it has been already shown that the various types of moorland on the Pennines are readily distinguished by the water coefficient of the peat.[1] On the *Eriophorum* moor, for example, its value generally ranges between five and seven though it may touch eight when the peat is composed of *Sphagnum*. An even higher value has been found on the lowland mosses of Lonsdale where the dominancy of *Eriophorum vaginatum* is disputed by *Scirpus cæspitosus*. Pools choked with living *Sphagnum* are of frequent occurrence and the peat is at times more than saturated with water so that the coefficient here attains its highest possible value. This has been confirmed experimentally, for when the peat has been saturated with water in the laboratory, its maximum water capacity has been found to be identical with its water-content *in situ*. What an enormous difference can be brought about by even partial drainage of the habitat is illustrated by a comparison of the two analyses below showing (1) the superficial layer possessed by *Calluna* and (2) the

[1] Crump, W. B. "The Water-Content of Acidic Peats." Report of the British Association, Portsmouth Meeting, 1911; *Naturalist*, 1911, pp. 361-2.

undrained moss occupied by *Eriophorum* or *Scirpus*. It is noteworthy that both these habitats may exist side by side, or rather superimposed, the surface roots of the *Calluna* never penetrating the saturated peat a few inches below the surface.

No. 166. Moss at Gilpin Bridge, Westmorland, August, 1911.

	Air-dry Peat.		Water.
	Water at 15°C.	Humus.	Humus.
Calluna on surface at 2-5 ins.	112·5%	71·5%	1·57

No. 165. Foulshaw Moss, Westmorland, August, 1911.

	Air-dry Peat.		Water.
	Water at 15°C.	Humus.	Humus.
Eriophorum, &c. at 6-8 ins. ...	865·2%	75·6%	11·4

The *Calluna* Moor is dealt with at length at a later stage. But one example may be quoted here to serve as an illustration of the average conditions, and for comparison with the next analysis.

Calluna vulgaris on *Calluna* Moor, Yorks., August, 1910.

	Air-dry Peat.		Water.
	Water at 15°C.	Humus.	Humus.
106 i. Compact peat at 1-2 ins.	78·4%	32·2%	2·43
ii. Ditto at 2-4 ins. ...	81·9	37·0	2·21
107. Coarse sand at 4-6 ins.	7·7	3·0	2·53

The Heath Formation. Though this may approach the *Calluna* Moor on the one hand, its drier examples stand out in strong contrast as shewn by the following case where *Erica cinerea* was the dominant plant and the light sand had hardly any covering of peat.

Sandy Heath at Bournemouth, August, 1909. *Erica cinerea*, with *Calluna*, *Molinia* and Pines.

	Air-dry Soil.		Water.
	Water at 15°C.	Humus.	Humus.
82. Sand at 4 ins.	20·2%	25·6%	0·78
83. Same at 6 ins.	8·0	9·1	0·88
84. Another at 4-5 ins. ...	11·0	13·8	0·79

Sessile Oak Wood Association. The analyses of Nos. 193-197, already given, show the range of soil moisture met with in an oak wood. Further examples are now quoted to illustrate the seasonal variation of the coefficient.

Complementary Society of *Pteris* and *Scilla* in Oak Woods, Yorks.

	Air-dry Soil. Water at 15°C.	Humus.	Water. / Humus.
A.—March, 1911.			
128. *Pteris* rhizomes, humous soil at 4-5 ins.	76·8%	19·7%	3·9
129. *Scilla* bulbs, stiff sand, at 8-9 ins.	37·0	8·3	4·47
B.—May, 1911.			
141 i. *Pteris*, humus at 6-8 ins. ...	176·6	64·7	2·7
ii. Ditto, sandy soil at 8 ins.	59·2	20·8	2·8
142. *Scilla*, stiff sand at 10-12 ins.	29·0	7·1	4·1
C.—July-August, 1911.			
153 i. *Pteris*, shale at 3-5 ins. ...	20·0	10·2	1·97
ii. Ditto ditto at 5-6 ins. ...	17·3	9·1	1·90
174. *Scilla*, stiff sand at 6-8 ins.	11·0	5·9	1·87

The problem is here decidedly complex. The bracken, whose rhizomes lie at the junction of two very distinct soils, has a vegetative period extending through the season covered by the analyses. The bluebells, whose bulbs are deeper seated have become dormant and independent of water-supply before the date of the third set. But the selected examples, few as they are, are sufficient to indicate and interpret the habitats. It is true that the seasonal drying is partially reflected in the water-content. But the coefficient demonstrates it much more accurately, showing a drop by August to half its value in the Spring. Further it eliminates entirely the diversity displayed in the layers occupied by the bracken (141 i. and ii.) The zone occupied by the bluebell bulbs has a high coefficient throughout the vegetative season, whereas the bracken has to endure at least a partial drought before the end of the season.[1] All this is in strict accordance with the known preferences of these plants, but the water-content does not suggest that the bluebell habitat is physiologically the wetter one and remains so as long as necessary.

Another pair of comparable habitats, examined on the same day, will suffice to prove the utility of the coefficient of humidity in distinguishing the ground societies within a wood.

[1] With a more extended series of analyses the method developed in Section VII could be applied to these woodland soils and would involve some revision of the values of the coefficient.

Deschampsia flexuosa, dominant on grit boulders and growing in fine sandy humus, Yorks., August, 1911.

		Air-dry Soil. Water.	Humus.	Water. / Humus.
170.	At 2-4 ins....	33·3%	44·0%	0·75
172.	At 3-4 ins....	24·8	25·3	0·98

Bromus giganteus, in sandy alluvium on edge of a stream, Yorks., August, 1911.

		Air-dry Soil. Water.	Humus.	Water. / Humus.
173 i.	Humus in ball of roots...	125·0%	25·4%	4·9
ii.	Stiff sand below ...	29·1	5·3	5·4

Though the water-content of 173 ii. lies midway between that of 170 and 172 the coefficient separates the two habitats in the clearest possible way. The woods characterised by stretches of *Deschampsia flexuosa* were first distinguished as "Dry Oak Woods" in the *Flora of Halifax*. The distinction was then based upon the nature of the vegetation, but it is now confirmed by analysis of the soil.

The Calcareous Formation. Through lack of opportunity calcareous soils have not, as yet, received much attention, and it is not safe to draw comparative inferences from a limited number of samples, all taken under the exceptional conditions of the summer of 1911. But the utility of the coefficient of humidity is still apparent.

Calcareous Grassland.

Sesleria cœrulea, in crevices of limestone rocks, North Lancs.

		Air-dry Soil. Water.	Humus.	Water. / Humus.
132.	April, 1911	31·4%	37·7%	0·80
135.	,, ,, ...	15·4	17·0	0·90
162.	August, 1911	22·3	19·0	1·17

The values of the coefficient are quite consistent in spite of the difficulty of obtaining uniform samples from the pockets filled with limestone chips, whilest the roots penetrate far into the crevices. The slightly higher value in August, in spite of the long drought, is of no importance. It merely indicates a local variation, a crevice more protected from evaporation. But it must be remembered that the Spring is often a season of drought. At the time when 132 and 135 were taken there had been practically no rain for six weeks. So the analyses point rather to uniform conditions and a low humidity in these limestone crevices.

The concluding set is of special interest because it gives the minimum value of the coefficient determined under natural conditions as well as values obtained earlier in the season, though from widely separated localities.

CALCAREOUS WOODLANDS.

Mercurialis perennis in Ash-Oak Wood on Mountain Limestone, North Lancs.

		Air-dry Soil. Water.	Humus.	Water. / Humus.
133.	April, 1911	66·2%	27·1%	2·44
160.	August, 1911	13·3	10·2	1·31

Mercurialis perennis wilting in Beech Hangers, on the chalk escarpment, Hants., September, 1911.

		Air-dry Soil. Water.	Humus.	Water. / Humus.
186	In different woods ...	9·7%	13·6%	0·72
187	In different woods ...	12·8	17·6	0·73
188	In different woods ...	10·6	10·6	1·00

Much more information must be collected before the conditions of the plant associations on calcareous soils can be compared fully with those of siliceous soils. But from what has been already set out it is clear there is no great disparity in the humidity of the habitats of *Deschampsia* on the grit and of *Mercurialis* on the limestone and chalk. Both appear liable to periods of considerable dryness and of about the same intensity.

The Sand-Dune Formation. The principle that the water-content is a function of the humus-content, that has so far been the sole condition for the determination of the coefficient of humidity, proves to be insufficient in the case of certain soils with a very low humus-content. In the case of sand-dunes, where the humus is less than 1% and the water less than 5%, the ratio water/humus is both high and irregular in value. Obviously this is because the water held by the sand particles is no longer a negligible fraction of the whole water-content. Though allowance might be made for this disturbing factor either experimentally, or by the consideration of a sufficiently large number of analyses, its influence was first detected in another field. As this appears to afford a solution of the problem it appears desirable to use this material for a more critical examination of the coefficient of humidity and this is done from a mathematical standpoint in the succeeding part of this paper.

Heather Moor Association. This habitat is selected for a more searching examination of the soil humidity because whilst the

association is very uniform over wide areas the humus-content varies considerably with the depth. The peat is as a rule so shallow that the heather roots regularly pass through it into the underlying coarse sandy soil that may be conveniently called the "sub-peat." The actual water-content of these two layers is not comparable, but physiologically the two seem indistinguishable, so that any satisfactory index of the humidity should have the same value for the two layers and thus be independent either of depth or humus-content.

This heather moor, as developed on the Pennines is a well-known association. The analyses available represent a number of localities in west Yorkshire, and cover the average seasonal range. To make the association more definite, the wetter type of heather moor characterised by the presence of *Erica Tetralix* is excluded from the present enquiry.

The results of the analyses are set out in the following table in order of the humus-content. As elsewhere in the paper the figures i., ii., iii. added to the soil numbers indicate corresponding layers of a section. There is no difficulty in distinguishing a peat from a sub-peat for the table shows that there is a sharp break between the two. It includes only one sample with a humus-content between 10% and 25%, so that whilst a sub-peat contains less than 10 or 15%, a peat never contains less than 25% and rarely less than 30% of humus.

HEATHER MOOR (*Callunetum vulgaris*).

PEATS: at 1 to 3 inches from the surface.

No.	Date.	Moor.	Water Loss at 15° %	% of Air-dry Peat.			Water. / Humus.
				Loss at 100°	Humus.	Mineral Residue.	
			y		x		m
207 i.	April, 1912	Greetland	168·2	12·2	70·8	16·9	2·4
206 i.	,,	,,	135·8	10·7	62·9	26·4	2·16
37	Mar., 1906	Cold Edge	139·4	7·2	49·6	43·2	2·8
99 i.	Aug., 1910	Norland ...	101·4	8·7	48·6	42·6	2·1
63	Aug., 1906	Rumbles...	99·1	7·3	40·0	52·7	2·5
205 i.	April, 1912	Greetland	83·9	7·2	38·4	54·4	2·2
58 i.	June, 1906	Bellhouse	90·8	5·7	37·6	56·7	2·4
106 ii.	Aug., 1910	Erringden	82·0	6·5	37·0	56·5	2·2
11	Sept., 1905	Greetland	73·0	5·6	36·5	57·9	2·0
58 ii.	June, 1906	Bellhouse	71·3	5·0	33·4	61·6	2·1
106 i.	Aug., 1910	Erringden	78·4	6·4	32·2	61·4	2·4
38	Mar., 1906	Cold Edge	84·7	4·8	30·7	64·6	2·76
57	June, 1906	Bellhouse	79·3	5·1	30·0	64·9	2·6
145 i.	June, 1911	,,	45·9	4·7	26·8	68·4	1·7
Mean		... ...	95·2	6·9	41·0	52·0	2·31

HEATHER MOOR *(Callunetum vulgaris).*

SUB-PEATS: at 2 to 5 inches from surface.

No.	Date.	Moor.	Water Loss at 15° %	% of Air-dry Peat. Loss at 100°	Humus.	Mineral Residue.	Water. / Humus.
			y		x		m
102	Aug., 1910	Broadhead	36·6	3·1	14·3	82·5	2·5
58 iii.	June, 1906	Bellhouse	29·4	1·6	9·9	88·5	3·0
206 ii.	April, 1912	Greetland	25·0	2·0	8·3	89·7	3·0
145 ii.	June, 1911	Bellhouse	17·8	1·5	7·1	91·4	2·5
207 ii.	April, 1912	Greetland	20·3	1·3	6·1	92·6	3·3
205 ii.	,,	,,	20·5	1·2	5·9	92·8	3·5
105	Aug., 1910	Erringden	22·2	1·1	5·7	93·1	3·85
99 ii.	,,	Norland ...	16·2	0·9	4·7	94·4	3·2
205 iii.	April, 1912	Greetland	14·0	0·9	4·2	94·9	3·36
107	Aug., 1910	Erringden	7·7	0·7	3·0	96·3	2·5
Mean	... ...	... ...	21·0	1·4	6·9	91·6	3·17

An inspection of the tables shows that the water-content falls steadily with diminution of the humus-content in spite of variation in season and locality. The coefficient of humidity, as expressed by the ratio water/humus, has a mean value of 2·3 in the case of the peats and 3·0 for the sub-peats. There is here a decided difference, which will be considered presently, but within either division there is no great departure from its mean value. The extreme range in either case is about 3 : 2 and this clearly represents the seasonal variation under the conditions already laid down, namely that soils are only sampled after a spell of dry weather. The range could certainly be extended by including more extreme conditions. Analyses made in August, 1911, during the prolonged drought of that summer, yield decidedly lower values for the *Calluna* habitat. But though valuable in determining the minimum value of the coefficient their inclusion here would confuse the general principle.

VI.—DEDUCTION OF THE COEFFICIENT FROM THE INDIVIDUAL OBSERVATIONS.

Having obtained two series of numbers expressing the conditions of the Heather Moor as displayed in the peat and the sub-peat respectively, the question arises—what is the most suitable treatment of these experimental values to obtain a constant to express the humidity of the *Calluna* habitat? Are the variations from the mean value such as have been already anticipated as inevitable, from the

nature of the problem, and in no way invalidating the concept of a constant quantity expressed by the mean? If so what is the best method of deducing the mean value? On the other hand is there any unsuspected cause operating that can be detected and eliminated by mathematical analysis? In particular what is the cause for the higher value of the $\frac{\text{water}}{\text{humus}}$ ratio in the case of the sub-peats?

It is clear, in the first place, that the range of water-content and humus-content is so great even when the sub-peats are separated from the peats that no great importance can be attached to their average values as expressed by the arithmetical means. Still it is noteworthy how closely the means in the case of the peats approximate to the Rumbles Moor sample (No. 63) which is undoubtedly typical of the Yorkshire heather moor.

Attention may therefore be concentrated on the values of the coefficient of humidity expressed by the ratio $\frac{\text{water.}}{\text{humus.}}$

If for a given habitat

$$\frac{\text{water-content}}{\text{humus-content}} = \text{a constant}$$

we have simply a special case of the general equation of the straight line passing through the origin of rectangular co-ordinates x and y viz:—

$$\frac{y}{x} = m$$

$$\text{or } y = mx \quad \dots \quad \dots \quad \dots \quad (1)$$

where m=coefficient of humidity=tangent of the angle the line makes with the axis x.

If the line does not pass through the origin the equation becomes

$$y = b + mx \quad \dots \quad \dots \quad (2)$$

where b is the ordinate at the origin.

The points to be considered are whether the values set out in the last column of the tables conform to a straight line rather than some other curve; and if so, whether it satisfies equation (1) or (2), and then to find the value of m, and of b if required.

When the values of x and y (humus and water) are plotted the the points obtained are so irregularly distributed that it is difficult to decide the slope of the curve by inspection, or even whether it passes through the origin. But no curve other than a straight line corresponds with the points. So a trial may be made with a straight line drawn through the origin and making with the x axis an angle

whose tangent is the mean value of the coefficient of humidity so as to satisfy the equation

$$y = mx.$$

Using the values $m=2{\cdot}3$ for the peats, and $m=3{\cdot}0$ for the sub-peats lines are obtained that show the individual points almost equally distributed on either side of the lines. This should be the case and in the case of the peats no further analysis seems necessary and the equation $y=mx$ may be accepted provisionally as a satisfactory solution.

VII.—Reduction by the Method of Least Squares.

But in the case of the sub-peats there is an obvious objection to the acceptance of the same equation even when m has a different value. For, in any case, when $x=o$, according to the equation $y=o$, but as a matter of fact, when the humus in the soil is reduced to zero there is still some water held by the soil particles. So that for these soils, with humus-content below 10 or 15% it is necessary to fall back on the equation

$$y = b + mx$$

where b represents the residual water present in the soil independently of any humus.

It is impracticable to find the value of b by the usual method of making $x=o$, and hence $b=y$, because no soil is met with entirely devoid of humus. But the most probable value of both b and m may be calculated from the experimental results by the method of least squares—a method of greater refinement than the occasion requires, but the only one available. If the linear equation is written in the form

$$b + mx - y = o$$

the values of y calculated from the equation will differ from the experimental values y_1, y_2, y_3, corresponding to experimental values x_1, x_2, x_3. Let these differences be $\delta_1, \delta_2, \delta_3$. Then

$$b + mx_1 - y_1 = \delta_1$$
$$b + mx_2 - y_2 = \delta_2$$

The method of least squares shows that when the sum of the squares of these differences is a minimum the calculated values of the constants b and m are the best that can be deduced from the experimental results, supposing all the observations are of equal accuracy and may therefore be given equal weight.

To obtain the values of b and m in the linear equation

$$y = b + mx$$

the method of least squares furnishes the two equations

$$b = \frac{\Sigma x \cdot \Sigma xy - \Sigma x^2 \cdot \Sigma y}{(\Sigma x)^2 - n\Sigma x^2} \quad \ldots \quad \ldots \quad (3)$$

$$m = \frac{\Sigma x \Sigma y - n\Sigma xy}{(\Sigma x)^2 - n\Sigma x^2} \ldots \quad \ldots \quad \ldots \quad (4)$$

where n=the number of observations.

But if $b=o$ simpler equations may be obtained, for then

$$\frac{\Sigma y}{\Sigma x} = m \quad \ldots \quad \ldots \quad (5)$$

and from equation (3)

$$\Sigma x \cdot \Sigma xy = \Sigma x^2 \Sigma y$$

$$\therefore \frac{\Sigma y}{\Sigma x} = \frac{\Sigma xy}{\Sigma x^2}$$

$$\therefore \frac{\Sigma xy}{\Sigma x^2} = m \quad \ldots \quad \ldots \quad (6)$$

If then the curve passes through the origin there are two alternative methods of calculating the coefficient of humidity (m). Applying these methods to all the values of water-content and humus-content set out in the tables the following results are obtained:—

By Equations 5 and 6

		Coefficient of Humidity (m).	
	n	$\frac{\Sigma y}{\Sigma x}$	$\frac{\Sigma xy}{\Sigma x^2}$
Peats	14 ...	2·32	2·32
Sub-peats	10 ...	3·03	2·91

The two values of m are, in the case of the peats, identical in spite of considerable individual departures from this mean value. So the equation $y=mx$ affords a complete solution and the water-content is found to be a function of the humus-content, and of that alone. This is expressed by the coefficient of humidity.

In the case of the sub-peats the two values are not identical so that the simpler equation is again found to be insufficient. But turning to equations 3 and 4 the following values are obtained by their application to the analyses of the sub-peats:—

	Sub-peats.
Residual water (b)	4·8%
Coefficient of humidity (m) ...	2·33

Hence for the sub-peats

$$y=b+mx$$

and to deduce the value of the coefficient the water held by the soil particles, practically 5% of the air-dry soil, must first be deducted

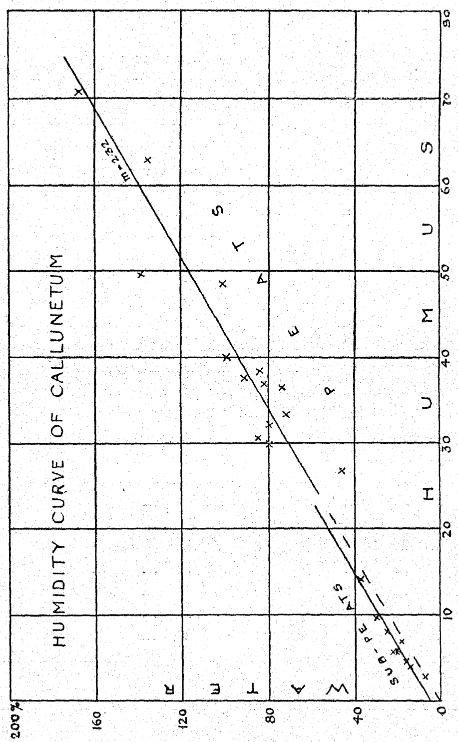


FIG. 1. Humidity Curves drawn from the values deduced by the Method of Least Squares.
(i) Peats — Coefficient of Soil Humidity = 2·32.
(ii) Sub-peats — Coefficient = 2·33, Residual Water = 5%

and then the remaining water is a function of the humus. Not only is it a function, but it is the same function as in the case of the peats, for the value of the coefficient is the same in each group.

The question naturally arises whether this residual water (b) is itself a constant, or whether it is not a variable depending upon the percentage of earthy (*i.e.*, non-humous) matter in the soil sample. Practically it may be regarded as a constant because it only has to be taken into account when the soils contain upwards of 80 or 85% of earthy matter, so that any variation of the amount is too small to affect the quantity of residual water so long as that is itself as low as the value arrived at above. The nature of the soil particles is likely to have a much greater influence on its magnitude. The sub-peats examined are all coarse sands composed largely of quartz-grains and free, or nearly so, from clay. In this case the residual water does not exceed 5% of the air-dry soil. What it may amount to in the case of clay soils is still unknown.

Accepting 5% as a sufficiently accurate allowance, in each case it is now possible to deduct this from the total water-content of the sub-peats tabulated above and so obtain the true coefficient of humidity for each sample. The improvement affected by this deduction is apparent on comparing the values of the coefficient in the samples that include both peats and sub-peats.

Coefficient of Soil-Humidity in successive layers after deduction of Residual Water (5%).

Soil No.		m	Soil No.		m
58 i.	... ...	2·4	205 i.	... ...	2·2
ii.	... ...	2·1	ii.	... (3·5)	2·6
iii.	... (3·0)	2·4	iii.	... (3·4)	2·1
99 i.	... ...	2·1	206 i.	... ...	2·16
ii.	... (3·2)	2·4	ii.	... (3·0)	2·4
145 i.	... ...	1·7	207 i.	... ...	2·4
ii.	... (2·5)	1·8	ii.	... (3·3)	2·5

The uncorrected values of m for the sub-peats are placed within brackets.

Before finishing with the humidity equations it is perhaps worth while to enquire what values would be obtained in the case of the peats if the equation $y=b+mx$ applied to them. Using equations 3 and 4 the method of least squares gives the following results:—

	Peats.
Residual Water (b)	—1·5%
Coefficient of Humidity (m) ...	2·35

The value of m is nearly the same as that already established, but b instead of being *nil* has a small negative value. No physical meaning can be attached to the negative sign, and its appearance only illustrates the extreme delicacy of the method of least squares. The curve obtained by it is sensitive not only to deviations from the mean but to their positions in the set of observations. Here it is undoubtedly peat No. 145 i. that having a value below the average, depresses the curve slightly below the origin because of its position at the end of the list. For the purpose in view and with the data available in soil analyses the method of least squares is almost too refined an instrument. With only half-a-dozen analyses the numbers obtained by its use may be quite misleading. Though further investigation may lead to a revision of the values set out in this paper, the material employed seems sufficient to furnish a fairly close approximation to the true magnitude of the coefficient of soil-humidity in the case of the Heather Moor Association, and to establish the principles involved in its determination.

VIII.—The Influence of Clay on the Soil Moisture.

If the method already applied to non-humous soils to determine the water held by the soil apart from the humus is sound, it follows that if a soil contains clay this will partially control the water-content even when present in much smaller quantity. Though such an effect has been anticipated no data are yet available for determining the coefficient of soil-humidity in clay soils. Nor is it clear whether the coefficient could be taken as the ratio $\frac{\text{water-content}}{\text{humus} + \text{clay}}$ as the joint effect of the two colloids may not be equal to the sum of their individual water-holding power. There is also the difficulty that in clay soils the loss on ignition includes more than the humus.

But an important paper on "The Moisture Equivalents of Soils" [1] by L. J. Briggs and J. W. McLane, that has only come to the knowledge of the author after the completion of this paper throws considerable light on the subject. Briggs and McLane's "moisture equivalent" is the percentage of moisture a soil can retain when subjected to a centrifugal force about 3,000 times the force of gravity. The authors show that the magnitude of this moisture equivalent for any soil depends almost wholly and equally upon the clay and the humus present. The silt exerts an appreciable though smaller effect, but all the coarser particles show practically no retentive action.

[1] U.S. Department of Agriculture, Bureau of Soils, Bulletin No. 45, Washington, 1907.

Put as an equation their result is

$$M=0{\cdot}13\ C + 0{\cdot}62\ (D + E),$$

where M is the Moisture Equivalent

C=per cent of silt (0·05—0·005 *mm.*)

D=per cent of clay (0·005—0· *mm.*)

E=per cent of organic matter determined by the chromic acid combustion method.

Neither M nor E is identical with the constants adopted in this paper, but there is a general correspondence. So it seems likely that the water-content of a soil depends primarily, and approximately to an equal extent upon the clay and humus-contents. In the case of a clay soil then it may be anticipated that the equation

$$y=mx + nz$$

will hold good; or if n proves to have the same value as m

$$y=m\ (x + z)$$

where z is the percentage of clay.

Though the method of investigation and the types of soil are totally different in the two cases, the conclusions arrived at in the present paper receive independent confirmation in the results of Briggs and McLane's study of agricultural soils. Both deduce a linear equation to express the equilibrium under stated conditions; both point to the soil-moisture under such conditions being an adequate and simple index of the soil.

IX.—Ecological Considerations.

In conclusion it seems desirable to glance at the broader aspect of the problems involved in the present investigation of the soil moisture in relation to the plant association. If the coefficient of soil humidity is to be of service in ecology it will only be by a thorough study of definite habitats, and the lines on which this can be prosecuted to advantage may be indicated as follows:—

(1). The mean value of the coefficient of soil-humidity m is the most important constant to be ascertained for every association whose distribution and existence are determined by soil moisture. This mean value, obtained by methods already described, may be indicated by M.

(2). But the coefficient for every such association will prove to have a considerable variation from its mean value. Given a sufficient number of estimations this variability would be best expressed by the "standard deviation," but in actual practice it would be sufficient to ascertain the maximal and minimal values, say m_1 and m_2, of a considerable number of estimations. These

values m_1 and m_2 mark the limits of the association and are probably determined by competition with other associations whose M values are different.

(3.) There will also be a supra-maximal (m_1') and a sub-minimal (m_2') value of m for any association or its component members, determined not by competition, but by the physiological relations of the root-systems with the soil-water. When these values are reached and maintained the association can no longer continue to exist.

Opportunities for determining these supra-maximal and sub-minimal values may not be frequent, and usually they may not be distinguishable from the maximal and minimal values. But there are occasions when they cannot be ignored. The case already quoted where *Mercurialis* was wilting in September, 1911 is one in point, where the sub-minimum had been reached, for though the plants recovered it was only because the existing state was not maintained, and clearly there was no competitive factor. Again the gradual accumulation of peat may of itself raise the coefficient to such a supra-maximal value that the existing association can no longer maintain its position, just as artificial drainage may lead to the extinction of the association by reducing the coefficient to its sub-minimal value.

(4). The sub-minimal value of the coefficient for any association will represent, and be the appropriate expression of the echard.

(5). The soil moisture index of an association will be fully determined by finding the values of m_1, m_2, m_1', m_2' and M.

These considerations only hold good at present in cases such as have been considered, where the humus practically holds all the soil water, *i.e.*, where there is no "free" water in the substratum, nor sufficient colloid clay to affect the balance.

It only remains for me to express my thanks to Mr. A. G. Tansley for helpful criticism of the paper, for calling my attention to the work of Briggs and McLane and for the suggestions utilized in the closing paragraphs.

THE HEATH ASSOCIATION ON HINDHEAD COMMON.

BY

F. E. FRITSCH, D.Sc., PH.D.,

Professor of Botany, East London College (University of London),

AND

WINIFRED M. PARKER, B.Sc.,

Demonstrator in Botany, East London College (University of London).

[WITH PLATE V AND FOUR FIGURES IN THE TEXT].

THE following paragraphs give a brief account of an investigation into the heath vegetation on Hindhead Common, which is being carried out by the staff and students of the Botanical Department of the East London College. Although the investigation is at present only in a preliminary stage, it is hoped that a short account of what has been done may be of interest. The area concerned lies to the right of the road leading from Hindhead to Guildford (*i.e.*, on the side opposite to that on which the famous "Punch Bowl" is situated); it is well suited for the purposes of such an investigation, as it is traversed only by a few paths and is very little frequented. The area has been visited annually in July and, in the present year, also in January and April. Our aim for the present has been chiefly to map a representative portion of the vegetation and to commence studies on the re-colonisation of new ground.

The area is situated on the Hythe beds of the Lower Greensand. Soil borings show that beneath a surface layer of peat varying from 1½ to 3 in. in thickness there ordinarily lies a layer of dark (rather peaty) sand (4 to 5 in.) and then a stratum of fine light-coloured sand (5 to 6 in.); at some points this lower stratum is rather stony. There are indications that the character of the soil (especially as regards its degree of coarseness) varies somewhat on different parts of the heath, but our investigations on this point are at present insufficient. Over a very considerable portion of the area an inch or so of the surface of the soil is charred, hard and brittle; it is astonishing how long the soil appears to retain this mark of a former fire, which must in some cases be at least ten years old.

In preparing the map (Text-fig. 1) the method adopted has been that of laying out the ground into 100 feet squares[1] and mapping each separately. The part of the area dealt with in the present account (cf. the map and the two sections, Text-figs. 1 and 2) comprises about half the Hindhead Common proper. It consists of a flat-topped central ridge, skirted by two valleys (A and B), each of which is traversed by a narrow (little used) pathway; the broad central ridge is totally undisturbed except for a clearing about 12 ft. wide extending along its whole length.[2] The two valleys exhibit a gradual downward slope towards the south-west and are bounded on one side by the steep inclines of the central ridge and on the other side by equally steep slopes—as shown in the sections (Text-fig. 2), in which, however, the vertical scale is exaggerated. The central ridge has a broad, almost flat top, the width of which gradually diminishes in the south-westerly direction (cf. especially the sections), where the ridge ultimately slopes down rapidly to the path connecting valleys A and B. The north-easterly part of this ridge is a broad flat plateau and does not begin to slope appreciably in the south-westerly direction until a point about 1,000 ft. from the top of the area shown in the map is reached; after that the slope towards the south-west is very gradual for a time, until near the end of the ridge a steep incline leads down to the path connecting valleys A and B at the extreme south-west end of the area.

A.—Constitution of the Heath Vegetation.

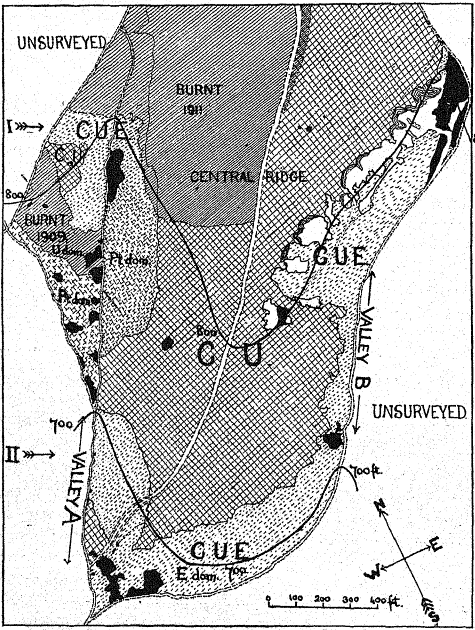
The valleys are partly occupied by a dense growth of tall *Ulex europæus* with very extensive tracts of high-growing bracken (*Pteridium aquilinum*); intermingled are a number of other woody species (especially *Rhamnus Frangula* and *Ulex minor*), together with a considerable number of herbaceous forms (cf. below, p. 156). The distribution of *Ulex europæus* on the area concerned quite agrees with other observations on the occurrence of this species on heaths.[3] It is practically confined to the neighbourhood of the pathways, from which however at some points it extends for some distance upwards on to the slopes of the valleys. A very few isolated patches are found on the top of the ridge, their presence there being at present difficult to explain; but these patches are really quite

[1] Oliver, F. W., and Tansley, A. G. "Methods of surveying vegetation on a large scale." New Phytologist, Vol. III, 1904.

[2] A second smaller clearing (not shown in the map) was made in the autumn of 1911.

[3] Tansley, "Types of British Vegetation," 1911, pp. 105-106. *Cytisus scoparius* shows a similar, but more limited distribution, being found only in the lower part of valley A on either side of the pathway.

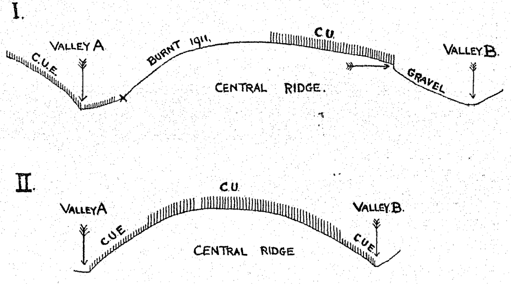
insignificant as compared with the extent of the remaining vegetation.



Text-fig. 1. Map of part of Hindhead Common at present surveyed. Pathways indicated thus =:=:=, clearings indicated thus = = =. The contours are indicated by heavy lines, and have been transferred from the Ordnance Survey maps. Areas of the common recently burnt are closely shaded. The black patches mark the positions of more or less extensive groups of *Ulex europæus*. The unshaded areas on the eastern slope of the central ridge represent exposed tracts of gravel (cf. Text-fig. 2). C U, *Calluna-Ulex* facies (cf. p. 153); C U E, *Calluna-Ulex-Erica* facies (cf. p. 154): Pt., *Pteridium aquilinum*. The thin irregular line running almost vertically through the area burnt in 1911 marks the former limit of the C U and C U E facies in this region.

The distribution of *Ulex minor* Roth (= *U. nanus* Forster) is very different from that of *U. europæus*. Together with *Calluna*, it is the dominant feature of the vegetation over the greater part of

the heath. Two (if not three) forms of this species must be distinguished. In the valleys, along with *U. europæus*, there grows



Text-fig. 2. Diagrammatic sections of the part of Hindhead Common at present surveyed. The points at which the sections are taken are indicated by arrows at the left-hand side of the map on the opposite page. The cross to the right of Valley A shows the position of the former limit of C U and C U E facies before the fire of 1911. The horizontal scale is the same as that of the map; the vertical scale is exaggerated. The horizontal arrow in section I. indicates the point at which the land-slide (p. 161) has taken place.

an upright form, differing markedly in habit from that usually described in floras. This upright form has generally no procumbent branches whatever, but an uprising main stem, varying in height from 2¼ feet to 4 feet.[1] The lower part of the main stem is mostly unbranched, while near the top numerous branches arise. Among the growth of low *Calluna* on the slopes of the valleys another form is found. In this case branching generally takes place freely from the base of the plant, the branches being for the most part procumbent. Occasional specimens, however, show one or more upright (or obliquely ascending) shoots, which grow to a height of 1½-2½ feet; these upright shoots (generally bare below and well branched above) are quite similar in habit to the upright form found in the valleys, and are the only part of the plant that appears above the level of the surrounding heath-vegetation.

As already indicated it is only occasional specimens of *Ulex minor* on the valley-slopes that show the upright shoots just described; a large number of specimens are entirely procumbent and of the type usually described in floras. In the zone of tall *Calluna*, found on the top of the central ridge, (cf. below, p. 152) the completely procumbent type is decidedly more prevalent than on

[1] The tallest specimen measured was 4 feet 2 inches high.

the valley-slopes, although even on the top of the ridge occasional specimens with upright branches occur, these branches however never arising above the *Calluna*-level. It must be realised therefore that over the greater part of the Hindhead heath the *Ulex minor* is hidden from view by the growth of other constituents of the vegetation and is only visible at close range. At many points the branches of the procumbent form give rise to compact cushions, almost completely hiding the underlying soil by their dense branching. Such cushions are beautifully seen on areas recently burnt (Pl. V, fig. 4) and on the exposed gravel slopes on the north-eastern side of the central ridge (cf. below, p. 162).

The following forms of *Ulex minor*[1] can thus be distinguished on the Hindhead heath:—(a) the normal procumbent form, prevalent among the tall *Calluna* found on the top of the central ridge and at some other points, and very common on the valley-slopes; (b) an upright form, generally without procumbent branches, and found only in the valleys; (c) an intermediate form, showing both procumbent and upright branches, frequently found on the valley-slopes and more rarely on the top of the central ridge.

There appears to be a marked tendency towards the production of upright shoots in *Ulex minor*, but it does not seem except in the valleys and on the lower parts of the valley-slopes that they can long withstand the conditions to which they are subjected. The most acute of these will be the drying influence of the prevailing winds. Many of the upright branches, especially on the upper parts of the slopes, show more or less advanced stages of drying up, and it would seem as though in these positions only those upright branches ultimately survive as are well protected from the prevailing winds by dense growth of the surrounding heath-plants. Many of the "intermediate forms" (*c* above) will thus by dying away of their upright shoots ultimately come to be of the normal procumbent type. When the present investigations have been carried on a few years longer the problem of the different growth-forms of *Ulex minor* will be definitely solved.[2]

We may next proceed to consider the constitution of the heath-association on the area concerned. The top and the upper slopes of the ridge are occupied by a growth of very tall *Calluna* ($2\frac{1}{2}$-$3\frac{1}{4}$ feet high and 10-14 years old). Standing on the flat top of the ridge one sees a monotonous expanse of ling, interrupted by an

[1] On some of the other heaths in this part of Surrey the upright form of *Ulex minor* is much rarer.

[2] About fifty marked plants of *Ulex minor* are under observation.

occasional specimen of *Pinus* or *Betula* or one of the isolated patches of *Ulex europæus* above referred to. This vegetation is however not nearly as pure as it appears at first sight, for not only is the ground very largely occupied by the procumbent form of *Ulex minor*, but scattered plants of *Erica cinerea*, *E. Tetralix* and *Vaccinium Myrtillus* are to be found over the whole surface. Except for the *Calluna* and *Ulex minor* however no other form can be regarded as dominant (C U facies, cf. map). The growth of the ling on this part of the heath is very dense, for the plants, although their bases are quite widely separated from one another, branch very profusely above, so that the upper branches of adjacent plants are generally close together. A striking feature is the very uniform level of the top of this *Calluna*-zone. This appears to be due to the fact that projecting tips, which grow beyond the level of the surrounding growth, tend to dry up and die away—a fact, which may be in part responsible for the very profuse branching exhibited by the plant in its upper portion. It is probable that the vertical growth of this tall *Calluna* takes place very slowly, although we have no satisfactory data as yet on this point.

Except where *Ulex minor* covers the ground there is thus plenty of room for the growth of other plants, but this growth has to take place under the shade of the *Calluna*, and the conditions are evidently not favourable.[1] *Erica* and *Vaccinium* are chiefly found where there is a break in the general continuity of the *Calluna*-level, whilst where the latter grows densely, the ground often bears no growth except for Mosses (*Polytrichum juniperinum*, more rarely *Leucobryum*) or Lichens (chiefly species of *Cladonia*). Bracken is altogether wanting over considerable areas of the ridge-top, and, when present, is represented only by isolated plants or small patches, the fronds of which rise to only about half the height of those in the valley. It is probable that the ridge-vegetation illustrates the oldest phase of the heath on the area under discussion (cf. below, p. 161).

This *Calluna-Ulex* vegetation extends downwards for a varying distance on to the slopes of the central ridge, but is terminated by a sharp limit (no doubt representing the line of termination of a heath-fire), visible even from afar (cf. Pl. V, fig. 1). In the lower half of the area concerned the C U facies extends down at some points to near the bottom of the valleys, actually reaching the path in valley A for a stretch of about 200 feet. A small distinct patch

[1] cf. Tansley, loc. cit., p. 104.

of the C U facies is also found along the path in valley A at the point where the clearing from the central ridge reaches this path (cf. the map).

Below the limit of the *Calluna-Ulex* vegetation the north-western, south-western and south-eastern slopes of the ridge bear a dense vegetation in which *Calluna*, *Ulex minor*, *Erica cinerea* and, to a lesser extent, *Vaccinium Myrtillus* compete for dominance (C U E facies). The *Calluna* in this region rarely exceeds a foot in height and is about five years old. *Ulex minor*, though largely procumbent (cf. above, p. 151), shows rather frequent uprising branches, such specimens alone appearing above the level of the surrounding *Erica* and *Calluna*. Bracken is much commoner (and provided with rather taller fronds) over the whole of this area than on the ridge-top, and for a stretch of about 600 feet in the middle of the north-western slope becomes a dominant, the green sheet formed by its fronds in summer being a very conspicuous feature. Specimens of *Pinus sylvestris*, *Rhamnus Frangula*, *Betula alba*, *Pyrus Aucuparia*, *Pyrus Aria* and *Ilex Aquifolium* are scattered in this low *Calluna*-zone, being generally more abundant on the lower parts of the slopes, especially near the lower end of valley A. Their presence however in no way affects the general character of the heath-vegetation among which they occur. The abundance of young plants of some of these species (especially *Betula*, *Pinus* and *Rhamnus*) at some points indicates a trend in the direction of a birch-heath. On the south-western slopes *Erica cinerea* becomes a dominant,[1] the heath at this point in July appearing as one purple stretch, when seen from a distance.

On the opposite (south-east) slope leading down to the valley A we have a repetition of the vegetation on the north-west slope. Most of this region is occupied by the C U E facies with dominance of *Pteridium* for a stretch roughly corresponding with that on the north-west slope. Only a small patch of the C U facies is found near the path on the extreme left of the map.

A number of grasses occur on the heath (*Deschampsia flexuosa*, *Molinia cærulea*, *Triodia decumbens*, *Agrostis canina*), but of these only the first two play a really important part. *Deschampsia* is on the whole most abundant on the top of the ridge and on the upper part of the slopes, while *Molinia* is found more especially in the valleys and along the sides of the slopes. Analyses have shown

[1] This dominance of *Erica cinerea* on southerly and south-westerly slopes is a general feature in this part of Surrey. Standing on Gibbet Hill in July nearly all the southern slopes visible from there appear a deep purple.

that the water-content of the soil is appreciably less on the top of the ridge than on the sides of the slopes and in the valleys, and it is possible that this factor determines the distribution of the two important grasses, although we should not like to accept such a conclusion without further evidence. It will be well at this point to refer to the distribution of another member of the heath-vegetation. In the heaths of other parts of England *Erica Tetralix* appears to favour the damper places. We can find no evidence of this on the heath at Hindhead, for this species shows no special restriction to certain points, and is, if anything, most abundant on the relatively dry summit of the ridge.[1]

There is no difference in specific constitution between the different facies of the *Callunetum* on the Hindhead heath, but, as the above description will have shown, the relative grouping of the species varies. The following is a complete list of the members of the *Callunetum*, found on the area at present mapped:—

Calluna vulgaris	*Molinia cœrulea*
Erica cinerea	*Triodia decumbens* (rare)
„ *Tetralix*	*Rhamnus Frangula*
Vaccinium Myrtillus	*Betula alba*
Ulex europæus (only isolated patches)	*Cratægus monogyna* (rare)
	Pyrus Aucuparia
„ *minor*	„ *Aria*
Potentilla erecta (isolated)	*Ilex Aquifolium*
Cuscuta Epithymum (rare, cf. p. 159)	*Pinus sylvestris*
Agrostis canina (rare)	*Pteridium aquilinum*
Deschampsia flexuosa	*Blechnum Spicant* (rare)

Along the edges of and in the immediate neighbourhood of the pathways a much larger number of species are found. Some of these are "weeds" but many are characteristic of southern *Calluna*-heaths[2] or of grass-heaths[3], but on the Hindhead Common are either strictly confined to the paths or only penetrate into the heath proper for a distance of 20–30 feet at the utmost from the paths. The following is a list of these species:—

[1] On the part of Frensham Common lying in the neighbourhood of the Little Pond, however, *Erica Tetralix* shows a decided preference for the damper ground. The heath on this part of the common consists of practically nothing but low *Calluna* (about 1 foot high) with an almost complete covering of *Cladonia* on the soil. In the neighbourhood of the water, however, *Erica Tetralix* appears in abundance, at some points even extending right into the marsh bounding the pond.

[2] cf. Tansley, Types, p. 105.

[3] Tansley, pp. 95, 96.

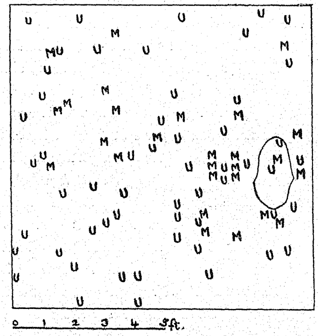
Anemone nemorosa
Viola tricolor
Cerastium viscosum
Stellaria graminea
Spergularia arvensis
Hypericum pulchrum
Ulex europæus (cf. p. 149)
„ *minor* (upright form, cf. p. 151)
Cytisus scoparius (cf. p. 149, footnote)
Trifolium pratense
Rubus spp. (incl. *R. Idæus*)
Potentilla erecta
Galium saxatile
Achillea Millefolium
Hieracium boreale (agg.)
Hypochæris radicata
Erigeron canadense
Centaurea nigra
Chrysanthemum Leucanthemum
Solidago Virgaurea
Campanula rotundifolia
Veronica officinalis
Digitalis purpurea
Teucrium Scorodonia
Plantago lanceolata
„ *major*
Rumex Acetosella
„ *crispus*
„ *obtusifolius*
Carex sp.
Anthoxanthum odoratum
Agrostis alba
„ *vulgaris*
Festuca ovina
„ *rubra*
Holcus lanatus
„ *mollis*
Bromus madritensis
„ *mollis*
Lolium perenne
Cynosurus cristata
Dactylis glomerata
Juncus effusus

Apart from these, all the members of the *Callunetum* (except *Pinus* and *Blechnum Spicant*) occur more or less abundantly in the immediate neighbourhood of the pathways. Near the upper end of valley A (but below the burnt zone) the *Callunetum* is extending across the narrow pathway to the elimination of the other forms previously found there.

B.—Recolonisation on the Hindhead Heath.

A considerable number of observations have been made on the recolonisation of burnt portions of the heath. A small area of the common situated on the south-eastern slope of valley A had been burnt some little time (1909) before we commenced work and a much larger portion (the greater part of which had already been mapped) was burnt in August, 1911. The latter may be considered first. Vegetation soon reappears on such burnt areas. As early as January (1912) *Ulex minor* (also *U. europæus* in the valley) was found sprouting afresh, while numerous seedlings of *Ulex* were growing on the ground. A considerable area of the burnt ground bore a growth of *Pyronema confluens*, but apart from this and the *Ulex* there was no other vegetation. In April of this year the fungus

had disappeared, but otherwise the vegetation of the burnt patch showed little change. On some parts of the burnt area nearly every plant of *Ulex minor* was sprouting from the base, the new growth being very closely adpressed to the surface of the ground as a general rule (cf. p. 152 and Pl. V, fig. 4); at other points the *Ulex*-plants over an area of two or three square yards showed no sign of resuming growth. Numerous *Ulex*-seedlings were present, but their number in comparison with January seemed to have diminished, and from other observations it appears very probable that only very few of them prosper. At some points on the burnt patch *Molinia* was reappearing, this growth again arising from the old plants (Text-fig. 3). Here and there very isolated fronds of *Pteridium* were



Text-fig. 3. Chart to show recolonisation on burnt heath; April, 1912. Every plant is indicated. M, *Molinia*; U, *Ulex*.

coming up, but no other forms yet showed any indication of growth. By July of this year a vigorous growth of the sprouting gorse had taken place, sufficient to give a greenish tinge to the whole area when viewed from a little distance. The seedlings of *Ulex minor* were however doing rather badly and gave no great promise of future success. This is in marked contrast to the behaviour of the seedlings of *U. europæus* on the part of the burnt area situated in the valley A; many of these looked very robust and had attained a height of 6-8 ins. above the level of the ground, their growth being no doubt favoured owing to the protection afforded to them by the dense mass of tall bracken that occupies the valley (cf. above). A considerable number of *Vaccinium*-shoots were now

arising from the old plants on the burnt area, and an occasional sprouting *Calluna* and *Erica* were also observed, while seedlings of the two last-named forms, and especially of *Erica* were rather numerous at some points.[1] Most of the old *Calluna* and *Erica*-plants however still showed no signs of life.

It may be added that although the area of ground burnt in 1911 included parts of both low and tall *Calluna*-zones (the former limit of which is shown on the map by a thin line), there was no outward difference in the method of colonisation over the whole region.

These observations tend to indicate that the typical heath-representatives are mainly stationary and reappear again in exactly the same positions as they occupied before a fire. A study of the small zone burnt before the survey was commenced leads to the same conclusions. This zone was first examined in July, 1910. At this time there were still appreciable pieces of bare, charred ground between the closely adpressed growth of the numerous *Ulex minor* plants which were sprouting from below. There was also a considerable growth of bracken, due to this burnt area lying within the zone in which *Pteridium* is a dominant (cf. above, p. 154). A few specimens of *Calluna* were found sprouting from the base of the old plants, and there were a considerable number of *Ulex* and some *Erica* and *Calluna* seedlings. A later examination (undertaken in April, 1912) showed that the ground had progressed further in the direction of the typical heath-vegetation. A good deal of sprouting *Erica cinerea* and *Vaccinium Myrtillus* was now present, so that by this time (probably about three years after the fire) all the typical representatives of the flora had reappeared, although the *Ulex* was still by far the most important form. While much of the *Erica* and *Calluna* had arisen from the old plants, there were quite a considerable number of young plants that had developed from seedlings—in fact in the case of *Calluna* it seems that its reappearance may be largely due to the development of seedlings and only to a smaller extent to sprouting from the old plants. In the case of the *Ulex minor*, however, a prolonged search is necessary to find a plant that

[1] It is interesting to compare the recolonisation of a part of the "Punch Bowl" that was also burnt in August, 1911. The vegetation on the burnt slope before the fire consisted of a dense growth with *Calluna*, *Pteridium* and *Vaccinium* as dominants, the two species of *Erica* as well as *Ulex minor* being quite scantily represented. In June of this year this area showed a great profusion of bracken, more strikingly developed than on the unburnt part close at hand. The next most important forms were constituted by the sprouting *Vaccinium* and by grasses. The scanty *Ulex*-plants were for the most part sprouting, but owing to their small numbers failed to give any stamp to the vegetation. The rather abundant *Calluna*-plants showed no signs of life.

has grown from seed,[1] and it is quite certain that the bulk of the numerous seedlings of this form, that first appear on such burnt ground, are unsuccessful.

The young growth on the burnt patch just described has been much infested with *Cuscuta Epithymum*[2] (cf. Pl. V, fig. 5, observed on *Erica cinerea*, *Calluna*, *Vaccinium*, *Ulex minor*). This parasite does not appear to make much headway subsequently, as it is almost absent from the greater part of the heath, although commonly found in the clearing on the top of the central ridge, where there is likewise abundant young growth of the heath-plants. It is noteworthy that on such young ground as is furnished by the burnt patches under consideration a number of species appear in small numbers, which are not found on other parts of the Hindhead heath. Some of these are characteristic representatives of other heath-floras (e.g., *Potentilla erecta*, *Teucrium Scorodonia*, *Carex pilulifera*).

The observations above detailed make it probable that the bulk of the plants appearing on such burnt ground owe their existence to the sprouting of new growth from the bases of the old plants, whose subaërial parts were destroyed by the fire. In this connection it is noteworthy that the species composing the *Callunetum* on the Hindhead heath (see the list on p. 155) are only those which can survive being burned over and over again, and this may account for the comparative paucity of the flora. It is probable that a number of plants are completely killed by the heat[3], and this may apply particularly to the relatively shallow-rooting *Calluna* and *Erica*, but even in these two cases a considerable number of plants certainly regenerate by sprouting. We thus obtain the conception of a possible repeated recovery from consecutive heath-fires, after each of which the vegetation passes through the preliminary phases indicated above, until it arrives at the stage of the fully developed heath. We have no doubt that the low *Calluna*-zone (C U E facies, cf. p. 154) marks a further phase in recuperation, in which the *Calluna* with a number of competitors is slowly attaining to complete dominance. We think that the final stage (as far at least as it is exhibited on the present area) is exemplified by the tall *Calluna*-zone occuring on the top and upper slopes of the ridge and at one or two other points (C U facies, cf. p. 153).[4]

[1] The main axis of these seedlings exhibits little growth and numerous prostrate laterals soon arise from its base, so that the procumbent habit is assumed at a very early stage.

[2] This also appeared this July on the *Ulex minor* on the ground burnt in 1911.

[3] *Ulex minor* sometimes fails to sprout over areas of several square feet.

[4] cf. Warming "Oecology of Plants" (1909), pp. 354-355

This last point requires some further consideration. In view of the fact that the C U facies is largely confined to the top and upper parts of the central ridge, it might be supposed that the C U and C U E owed their distinction to the slightly different habitats or to soil-conditions. These possibilities have not been disregarded, but there are, we think, important objections to such a view, which may be briefly summarised as follows:—

(i) The C U facies is not entirely confined to the top and upper slopes of the ridge, but at some points extends right down into the valleys (cf. p. 153 and the map). This is also true of other parts of the Hindhead Common, not included in the map (owing to their survey not being complete). Where the C U facies extends down into the valleys, an investigation of the soil has failed to show any difference from that inhabited by the adjacent C U E facies.

(ii) If the two facies were due to the difference of habitat, one would expect to find a gradual transition between them, since the conditions of the habitat do not change suddenly. As it is however there is a very sudden change from the C U E to the C U, so sharp that it can easily be seen half-a-mile away (cf. Pl. V, figs. 1 and 2, and p. 154). We have no doubt that this sharp line of demarcation marks the limit of a fire, since the recent fires have left just such a line at other points on the area.

(iii) The *Calluna* and *Ulex* in the C U facies are much older (10-14 years) than the *Calluna* and *Ulex* in the C U E (about 5 years old).

We think that these objections are sufficiently strong to make it very unlikely that the two facies are due to habitat or soil-conditions, and that they constitute good presumptive evidence for the view that the C U facies is merely a later stage of the C U E facies. Direct evidence is of course at present not obtainable, nor is it possible to say exactly how the transition is accomplished, But it appears probable that the dense branching of older *Calluna*-plants has a great deal to do with the elimination of the other constituents of the C U E facies. It may be recalled (p. 153) that where there is a break in the continuity of the *Calluna* on the ridge-top *Erica* and *Vaccinium* very often occupy the ground, and this tends to show that the habitat is quite suitable, but that these forms can only get on where they can escape the dense shade of the tall *Calluna*. As our observations progress year by year we hope to be able to collect the direct evidence, that will completely establish the correctness of the above view.

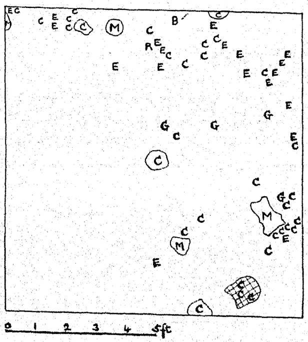
To summarise the preceding remarks we would distinguish the following four successive stages in the recolonisation of burnt ground on the heath at Hindhead. (a) Sprouting of the gorse. (b) Appearance of new growth from the base of other members of the heath-flora and development of a number of seedlings (gorse dominant). (c) *Calluna*, *Erica cinerea*, *Ulex minor* and to some extent *Pteridium* and *Vaccinium* competing for dominance (C U E facies). (d) *Calluna* (tall) and *Ulex minor* dominant, all other forms subsidiary (C U facies). Judging by the number of annual rings it would appear that the gorse-plants in the low and high *Calluna*-zones are almost invariably a year older than the corresponding *Calluna*-plants—an observation which indicates that also in these regions of the heath the gorse has been the first coloniser.

A word may be added on the behaviour of *Ulex minor* during the recolonisation of burnt ground. The shoots that arise from the old plants are at first all procumbent (Pl. V, fig. 4), but already during the first season following a fire upright branches appear on some of the plants. These upright branches however appear to grow but slowly in the first years, and it is only when *Calluna*, *Erica* and other forms are growing up all round that some of these upright shoots of the gorse begin to grow more vigorously and develop into the upright branches, described on p. 152. It is probably only those upright shoots that do not project far beyond the level of the surrounding heath that manage to survive the drying influence of the winds and that remain as upright shoots in the C U facies.

It is a familiar fact that after a heath-fire bracken often tends to appear in far larger quantity (cf. footnote on p. 158). As regards the area burnt in 1911, which bore very little *Pteridium* before the fire, there is some slight evidence of increase, but no very decisive proof can be adduced at present. The area burnt in 1909 lay largely within the zone in which bracken is a dominant, but here again we have hitherto failed to obtain any really decisive evidence of a marked increase. It may be pointed out that owing to the rapidity with which *Ulex minor* recolonises the ground, the bracken may not obtain those facilities for spreading its domain, which it finds on heaths not so largely occupied by gorse. We hope to be able to give further data on this point in later communications.

On the south-eastern slopes of the central ridge leading down to the valley B a number of land-slides have occurred some years back, whereby considerable stretches of yellow gravel of a rather coarse character have been exposed. This gravel extends to a depth

of about four inches, being followed by grey sand with stones. On this gravel-area are large patches of the C U facies that have slipped down bodily from above and grow on stretches of soil like that on the ridge-top. Some of these patches consist of pure C U, while on others *Erica cinerea* flourishes extensively; the latter are no doubt derived from more open parts of the C U facies, in which the *Erica* had managed to hold its own, and now on an isolated patch, removed from competition with the *Calluna*, exhibits a more extensive development. Between these patches there are large areas of exposed gravel, the recolonisation of which is very slowly proceeding, and a study of the process has proved interesting in comparison with the colonisation of the burnt areas on the heath. On the gravel everything depends on the success of seedlings. The vegetation is at present very open, large areas bearing little or no growth. Part of the gravel is being colonised by *Molinia*, large plants of which are very abundant at some points and act as a kind of sand-binder (Pl. V, fig. 3). At other spots numerous seedlings and young plants of *Erica cinerea*, *Calluna* and *Molinia* are found, whilst *Ulex* is relatively much less important (cf. Text-fig. 4). A



Text-fig. 4. Chart to show recolonisation on exposed gravel; April, 1912. The cross-hatched area marks a patch of *Ulex minor* in which three *Calluna* seedlings have developed. M, *Molinia*; E, seedlings of *Calluna*; C with an enveloping line, *Calluna* plants; G, young grasses (in part *Molinia*); R, seedlings of *Rumex*; B, a small patch of moss (undetermined).

considerable number of seedlings of *Rumex* occur. The seedlings of all these forms do not appear to make much progress, and it is evident that, except for the *Molinia*, colonisation goes on very slowly.

It is even now apparent that the vegetation, which will finally become established on the gravel, will bear a decidedly different aspect, at any rate for some time, to that on other parts of the heath; the Ericaceous forms (particularly *Erica*), as well as *Molinia*, will first be dominant, the gorse probably quite subsidiary.

In conclusion we should like to acknowledge our indebtedness to Mr. A. G. Tansley for much helpful criticism.

July, 1912.

EXPLANATION OF PLATE V,

ILLUSTRATING PAPER BY PROFESSOR FRITSCH AND MISS PARKER ON "THE HEATH ASSOCIATION ON HINDHEAD COMMON."

Fig. 1. End of central ridge, seen from a point corresponding approximately to the letter N in the right-hand lower corner of Text-fig. 1. The top of the ridge is occupied by the C U facies, which is separated by a sharp line from the C U E facies lower down. The vegetation in the foreground belongs to the slopes on the opposite (north-west) side of valley B.

Fig. 2. Line of separation of C U and C U E facies on the north-west side of the central ridge.

Fig. 3. Exposed gravel on south-eastern slopes of central ridge, partly occupied by *Erica cinerea* and *Molinia*. In the background extensive patches of C U, which have slipped down from the ridge above, are visible. The edge of the ridge is seen on the horizon.

Fig. 4. Burnt patch (burnt 1911), first year growth of *Ulex*. July, 1912.

Fig. 5. Burnt patch (burnt 1909). *Ulex minor* regenerating on burnt ground and infested by *Cuscuta*.

(Figs. 2, 3, 4 from photographs by Mr. W. B. Johnson; the rest from photographs by F. E. Fritsch.

ON VARIOUS METHODS FOR DETERMINING OSMOTIC PRESSURES.

WITH A DESCRIPTION OF THE APPLICATION OF BARGER'S METHOD OF DETERMINING MOLECULAR WEIGHTS TO THE ESTIMATION OF THE OSMOTIC PRESSURE OF THE CELL SAP OF PLANTS.

BY A. C. HALKET, B.SC.,

Demonstrator in Botany, Bedford College, London.

[WITH TWO FIGURES IN THE TEXT.]

I.—SOME METHODS OF DETERMINING OSMOTIC PRESSURE.

VARIOUS methods of determining osmotic pressure have been used at different times by workers investigating the properties of solutions of different kinds. A brief review of these may be useful.

1. *Plasmolytic method.* This method, which we owe to de Vries, has been the one generally employed to determine the value of the osmotic pressure of the cell sap of plants. Cells of the tissue under examination are placed in salt solutions of various known strengths and, as the solution which has exactly the same osmotic pressure as the cell sap causes no change to take place, that solution which causes just a slight shrinking of the protoplasm away from the cell wall is taken as isotonic (isosmotic) with the cell sap. This method is, however, not without its difficulties. Ewart[1] comments on this point in his paper "On the Ascent of Water in Trees," where he speaks of its want of exactitude for determining the osmotic pressure of the sap of small cells.

Some of the recent work on the toxic action of many of the common inorganic salts on the protoplasm of plant cells shows that plasmolysis of cells is induced by salt solutions of concentrations far weaker than those isotonic with the cell sap. Osterhout[2] reports that in young plants of *Vaucheria*, produced from zoospores, the protoplasm contracted away from the cell-walls when the filaments were immersed in a ·0937 gram-molecular solution of sodium chloride. Contraction of the protoplasm was also caused by a solution as dilute as ·0001 molecular if it was allowed to act for some days. This contraction was found not to take place if the

[1] "On the Ascent of Water in Trees." Phil. Trans. Roy. Soc., Vol. 199, 908, p. 355.

[2] "On Plasmolysis." Bot. Gaz., Vol. 46, 1908, p. 54.

salt solution was "balanced" by the addition of a little calcium chloride. Osterhout therefore suggests that the salt, sodium chloride, has some effect on the protoplasm which is not purely osmotic. True's[1] work on the physiological action of sodium chloride and potassium nitrate on *Spirogyra* cells also showed that these salts were not without some toxic action on protoplasm.

2. *Direct determinations.* The osmotic pressure of various solutions has been measured *directly* by means of a semi-permeable or differential membrane of copper ferro-cyanide, first by Pfeffer, more recently by Morse and Fraser[2] and others, and by Berkeley and Hartley.[3]

3. *Indirect determinations.* The value of the osmotic pressure of any solution is, however, generally determined *indirectly* by utilising some other function of the solution which also depends on the amount of substance in solution. The osmotic pressure, the vapour pressure, the freezing point, and the boiling point are all functions of any solution which vary with its concentration, and the osmotic pressure has been calculated (*a*) from the difference between the vapour pressure of the solution and that of the solvent (*b*), from the depression of the freezing point of the solution below that of the pure solvent, and (*c*) from the elevation of its boiling point above that of the pure solvent.

4. *Physiological methods.* Certain physiological methods have been used to estimate the value of the osmotic pressures of various solutions.

The action of salt solutions on the red corpuscles of blood has been utilised to find what strengths of the solutions are isotonic. This has been done in two ways; the concentrations of different solutions that cause "laking" of blood have been compared, and the amount of decrease in volume of the corpuscles in different salt solutions has been measured by means of the hæmatocrit, and compared.

The behaviour of certain bacteria in various salt solutions has also been used to determine what concentrations of these solutions are isotonic.

As far as I know the majority of these methods have not been used for any extensive determinations of the osmotic pressure of

[1] "The Physiological Action of certain Plasmolysing Agents." Bot. Gaz., Vol. 26, 1898, p. 407.

[2] Amer. Chem. Journ., 1905-1909.

[3] Phil. Trans. Roy. Soc., Series A, 1906.

the cell sap of plants. The great objection that can be brought against most of them is that a considerable quantity of liquid is required and this is difficult to obtain from many parts of plants. However, by one of the indirect methods mentioned above, utilising another physical property, osmotic pressures of cell sap have been determined.

Freezing point method. In these cases the osmotic pressure of the cell-sap has been calculated from the amount the freezing point of the sap is depressed below that of pure water. The ordinary Beckmann's thermometer generally used to measure these small differences in temperature is large and so necessitates the use of a considerable quantity of sap—10-c.c. to 20-c.c. A smaller form of thermometer requiring only 1·5-c.c. of liquid has been described by Guye and Bogdan.[1]

Sutherst,[2] seeking to account for the fact that plants were not always injured by frost, found the depression of the freezing point of the sap of certain plants below that of pure water. He used somewhat watery plants, *e.g.*, vegetable marrow, celery, cabbage, etc., reduced the tissues to a pulp by means of a grater and obtained the sap by filtering the mass. He found the freezing point using 5-c.c. of the sap and a freezing mixture of Glauber salts and concentrated hydrochloric acid. He did not, however, calculate the values of the osmotic pressures of the various saps.

Atkins[3] gives a number of determinations of the values of the osmotic pressures of the sap of many fruits, tubers, etc., calculated from the depression of the freezing point found, using Beckmann's thermometer.

Cavara[4] has also made an extensive series of estimations of the osmotic pressure of the cell sap of the stems, leaves and fruits of many plants making the amount of the lowering of the freezing point the basis for calculating the osmotic pressures.

Dixon and Atkins[5] have described a modification of this method

[1] "Méthodes rapides pour l'analyse physico-chimique des liquids physiologiques." Journ. Chim. Phys., 1903.

[2] "The Freezing Point of Vegetable Saps and Juices." Chem. News Vol. 84, 1901, p. 234.

[3] "Cryoscopic Determination of the Osmotic Pressures of Some Plant Organs." Proc. Roy. Dub. Soc., Vol. 12, 1910; also Notes from the Bot. School Trin. Coll. Dub., Vol. 2, 1910.

[4] "Risultati di una serie di rceriche crioscopiche sui vegetali." Contrib. Biol. Veg., Vol. 4, 1905, p. 41. (Abstract in Bot. Centr., Band 104, 1907, p. 547).

[5] "On Osmotic Pressures in Plants, and on a Thermo-Electric Method of Determining Freezing Points." Proc. Roy. Dub. Soc., Vol. 12, 1910; also in Notes from the Bot. School Trin. Coll. Dub., Vol. 2, 1910.

in which the change in the freezing point is measured, not by a thermometer, but by means of a galvanometer. The form of apparatus used requires 2·5-c.c. to 5-c.c. of liquid. The authors used their method to estimate the osmotic pressure of the expressed sap of the leaves of a number of trees. Dixon[1] has also estimated the osmotic pressure in leaves by placing shoots in a closed vessel containing some gas under high pressure and observing the pressure at which the leaves collapsed, *i.e.*, he found an external gas-pressure which balanced the internal pressure in the cells.

II.—Application of Barger's Method of Determining Molecular Weights to the Estimation of the Osmotic Pressure of the Cell Sap of Plants.

In view of the fact that all the purely physical methods of determining the osmotic pressure of the cell sap of plants hitherto employed [illegible] a comparatively large amount of cell sap or somewhat ela[illegible]paratus, I thought it would be of interest to put on recor[illegible]od I have used to determine the osmotic pressure of the cel[illegible] certain salt marsh and other succulent plants.

The method is a vapour pressure one and was invented by Barger[2] for estimating the molecular weights of small quantities of organic substances. The vapour pressure of the solution of unknown strength is compared with those of solutions of known strength. The vapour pressure of any solvent is lowered by the addition of any substance, and the amount by which it is lowered is proportional to the weight of substance present. As the osmotic pressure of any solution depends also on the amount of substance in solution and increases according to the amount of substance dissolved, the osmotic pressure of any solution varies inversely as the vapour pressure.

Barger states in his paper that the idea originated from an observation made during some experiments, on the adaptation of fungi to salt solutions, carried out in the late Professor Errera's laboratory in Brussels. The fungi were grown in hanging drops of solutions, the sides of the damp chambers being of cardboard kept moist with distilled water. The drops of solution were found to increase in size. This increase in size was explained by Professor

[1] "On the Osmotic Pressure in the Cells of Leaves." Proc. Roy. Irish Acad., Ser. 3, Vol. 4, 1896, p. 61.

[2] "A Microscopical Method of Determining Molecular Weights." Trans. Chem. Soc., Vol. 85, 1906, p. 287.

Errera to be due to the fact that, as the vapour pressure of the salt solution was lower than that of water, the water vapour in the air of the damp chamber condensed more quickly on the surface of the hanging drop, the stronger solution. The drop therefore increased in size at the expense of the water in the cardboard. Barger investigated the phenomenon quantitatively and found that the best way to estimate the amount of change that took place in the volumes of any two solutions was to put drops of the solutions in a capillary tube and measure their increase or decrease under a microscope.

The vapour pressure of the cell sap is compared with that of each member of a series of salt solutions of which the concentration is known. These salt solutions differ only slightly in strength one from another, so that there is one whose vapour pressure will be approximately equal to that of the cell sap, the solution under investigation. When such a solution is found it [illegible]ded as isotonic with the cell sap. The difference in vapo[illegible] the two solutions, the cell sap and one of the s[illegible] of known strength, is found by measuring the increase or d[illegible] in the size of the drops of the solutions in a capillary tube.

Capillary tubes about three inches in length are use[illegible], and are filled as follows. One end of the capillary tube is close[illegible] by one's finger and the other end is dipped into the solution [illegible] of known strength and a drop is allowed to run up the tube. The t[illegible] is then removed from the solution and a bubble of air is made t[illegible] enter it, and it is then placed in the cell sap and a drop of that is [illegible] allowed to run up, then another bubble of air, then another drop of t[illegible] solution of known strength and so on. The process is repeate[illegible] until the tube contains a number of drops of the two solutions [illegible] with each other, each drop being separated from the one [illegible] by a bubble of air. The size of the drops is regulated b[illegible] of the finger on the top of the tube. The first and last dr[illegible] should be of the solution of known strength, are made m[illegible] than the others. The number of drops is immaterial an[illegible] of convenience. When there are a sufficient number o[illegible] the tube, the ends are sealed up and the tube, for conv[illegible] handling and identification, is fastened to a microscope s[illegible] with Canada balsam or with soft sealing wax. Other[illegible] filled with one of the different members of the series of s[illegible] of known strength and the cell sap. The slide, when f[illegible]

is placed in a Petri dish containing water; this makes measurement easier and keeps the temperature constant. Fig. 1 shows the arrangement of the tubes, the black drops represent the salt solution of known strength, those shaded, the cell sap.

In this way in each tube there are a number of small chambers full of air, the end walls of each chamber being made by the surfaces of the two solutions. Evaporation of the solvent takes place from both surfaces into the closed air space, but condensation takes place more rapidly on the surface of the stronger solution. The drops of the stronger solution therefore increase in length while those of the weaker decrease.

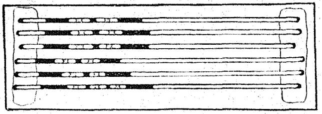


Fig. 1. For description see text.

As soon as the tubes are ready the lengths of the drops are measured. The first and last drops are not measured as their concentration may have been slightly altered when the ends of the tube were sealed. The drops are measured, under a low objective ($\frac{2}{3}$ inch) of the microscope, by means of a micrometer eye-piece. The middles of the menisci of each drop are focussed clearly and the distance between them read off on the scale. The appearance of the drop and the scale is shown in Fig. 2.

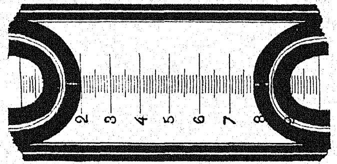


Fig. 2. For description see text.

The scale I used had 100 divisions. With care readings may be made to a tenth of one of these. Errors in reading were found not to exceed a fifth of one of the divisions.

After the drops are measured the tubes are set aside for some time. After an interval the drops are re-measured and the difference in length found. If the tubes have been carefully filled it will be found either, that in one tube of the series no change takes place in the size of the drops, or, as most frequently happens, that the drops of the cell sap increase in size when in tubes with solutions above a certain strength, while they decrease in size when with solutions below that strength. In the first case the solution with which no change takes place in the size of the drops is taken as isotonic with that of the cell sap. In the second case the mean between the known solutions, in the two tubes, is regarded as isotonic. Reference must be made to Barger's paper for further discussion of the method.

I first estimated the osmotic pressure of the cell sap of plants in this way while with Professor F. W. Oliver's expeditions to the Bouche d' Erquy in Brittany. During the course of the work there it was thought desirable to investigate the value of the osmotic pressure of the cell sap of some of the characteristic plants. The The greater part of the work was done on *Salicornia*. This is a very succulent plant, with a jointed stem and small opposite scale leaves. Underneath the epidermis there are two or three layers of small-celled palisade tissue, then a zone of aqueous tissue before the central strand with the vascular tissue is reached. The osmotic pressure of the cell sap was first estimated by plasmolysis, but this method was found to be satisfactorily applicable only to the cells of the epidermis and not to the cells of the aqueous tissue which are large and have no easily visible protoplasmic lining. It was therefore suggested by Mr. F. Baker, a chemist attached to the party, that it might be possible to use Barger's method for determining molecular weights in order to find the values of the osmotic pressure. The method was tried and found to be quite applicable, and many estimations were made.

Efficiency of Method. It was necessary to test the delicacy of the method, so a series of experiments was made to find whether the difference in the vapour pressures of solutions of sodium chloride in water, differing only slightly in strength, was sufficient to make the drops in the capillary tubes show any change in length. The solutions of salts generally used for the plasmolytic method vary in strength by ·01 of a gram-molecular solution. It was found that similar differences in strength could be detected by Barger's method. This is shown by the figures given below :—

FIGURES OBTAINED USING TWO SOLUTIONS OF SODIUM CHLORIDE DIFFERING FROM EACH OTHER BY ·01 OF A GRAM-MOLECULAR SOLUTION.

G.-MOL. STRENGTHS OF SOLUTIONS	(a) 1ST READING. (b) 2ND READING.	LENGTHS OF DROPS.				
1·59 & 1·58	(a)	78·0	65·0	55·5	84·4	48·5
	(b)	75·5	66·0	55·0	85·5	47·0
	Change	—	+	—	+	—
1·44 & 1·45	(a)	57·9	55·4	66·0	74·3	74·5
	(b)	58·3	54·9	66·8	74·0	75·1
	Change	+	—	+	—	+
1·43 & 1·44	(a)	77·5	93·4	71·0	84·4	80·7
	(b)	78·8	92·3	71·1	83·3	82·2
	Change	+	—	+	—	+
·2 & ·19	(a)	52·7	57·8	52·8	62·2	61·5
	(b)	51·9	58·5	52·1	63·0	60·8
	Change	—	+	—	+	—
·19 & ·18	(a)	62·2	41·4	45·9		
	(b)	61·5	42·2	44·9		
	Change	—	+	—		
·18 & ·17	(a)	47·7	52·5	74·7		
	(b)	46·6	53·5	73·3		
	Change	—	+	—		
·13 & ·14	(a)	41·3	44·3	41·5	32·5	46·7
	(b)	42·0	41·1	41·8	32·3	47·2
	Change	+	—	+	—	+
·12 & ·13	(a)	43·4	55·1	53·7		
	(b)	44·3	54·3	55·1		
	Change	+	—	+		
·12 & ·11	(a)	38·2	36·3	39·5		
	(b)	37·7	36·9	39·3		
	Change	—	+	—		
·11 & ·10	(a)	57·5	49·8	54·0		
	(b)	56·9	50·1	53·8		
	Change	—	+	—		
·08 & ·07	(a)	27·8	33·0	42·3	46·1	34·7
	(b)	27·2	33·7	41·3	46·8	34·1
	Change	—	+	—	+	—

This table shows the results obtained by balancing eleven pairs of solutions. The range of the concentrations is considerable, but the members of each pair only differ by ·01 gram-molecular solution. In each case the change that takes place shows quite definitely which of the two solutions is the stronger. On consideration of the figures it will be observed that the size of the drops does not vary

regularly, the drops do not increase and decrease by the same amount. The change is not quantitative, the result simply shows that the drops of the stronger solution increase in length while those of the weaker decrease. Experience has shown that in order to get this regularity of increase and decrease great care must be taken in filling the tubes. The drops must not be allowed to run up and down the tube during filling, for if they do so the solutions become mixed as there is always a film of liquid on the sides of the tubes. This mixing does not so much affect the change when the difference between the concentrations of the solutions is greater, but with small differences it prevents a satisfactory result being obtained. The time it is necessary to leave between the first and second readings also varies with the strength of the solutions used. If the solutions differ very much from each other in strength, two to three hours is all that is necessary, but if the solutions are nearly equal in strength, *e.g.*, ·12 and ·11 molecular solution, the tubes must be left for a longer time. It was generally found convenient to fill the tubes one day, measure the drops, then leave them all night and re-measure the drops the next morning.

Values of the Osmotic Pressures of Cell Sap Found by Barger's Method.

In the tables below are given certain values of the osmotic pressure of the cell-sap of some succulent plants obtained by this method.

Salicornia ramosissima (from water channel).

Gram-Molecular Concentration of NaCl.

1·0			1·1			1·2			1·3		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
38·0	42·9	+	15·8	19·1	+	35·1	34·0	—	18·0	15·6	—
75·0	69·8	—	40·0	38·9	—	38·0	39·0	+	35·8	36·8	+
27·8	34·7	+	26·1	28·3	+	21·9	20·0	—	18·9	16·4	—

The vapour pressure of the cell sap is less than that of a 1·1 gram-molecular solution of sodium chloride and greater than that of a 1·2 solution, therefore the osmotic pressure of the cell-sap is taken to be equivalent to that of a 1·15 gram-molecular solution of this salt, *i.e.*, to 45·6 atmospheres at 18°C.

Salicornia ramosissima (from higher ground).

Gram-Molecular Concentration of NaCl.

1·6			1·5			1·4			1·3		
1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.
16·3	15·2	—	21·3	20·5	—	17·4	19·7	+	23·9	24·4	+
30·8	31·2	+	33·8	34·7	+	47·5	46·7	—	53·4	52·7	—
13·2	10·4	—	25·2	20·6	—	25·8	30·3	+	11·3	11·7	+
									61·2	60·6	—
									24·1	24·6	+

Therefore the osmotic pressure of the cell sap is taken to be equivalent to that of a 1·45 molecular solution of sodium chloride, *i.e.*, to 56·53 atmospheres.

Cotyledon sp.

Gram-Molecular Concentration of NaCl.

·15			·14			·13			·12			·11		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
58·7	55·2	—	65·3	63·5	—	79·8	80·9	+	54·3	56·2	+	68·4	69·8	+
72·2	75·6	+	87·3	88·9	+	55·4	54·8	—	54·7	52·4	—	47·1	44·6	—
63·2	58·7	—	89.0	87·2	—	48·0	48·3	+	53·5	56·5	+	52·6	55·2	+
87·6	90·0	+	82·6	84·6	+	38·4	37·5	—	63·4	61·8	—	70·1	67·5	—
50·7	47·9	—	74·2	72·1	—	58·4	59·3	+	58·2	59·8	+	35·4	37·1	+

Osmotic pressure of cell sap is therefore equivalent to that of a ·135 molecular solution of sodium chloride, *i.e.*, to 5·9 atmospheres.

Clinia nobilis.

Gram-Molecular Concentration of NaCl.

·10			·09			·08			·07			·06		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
73·4	71·3	—	56·9	54·8	—	26·0	27·2	+	14·7	15·5	+	52·0	54·0	+
67·1	68·6	+	59·7	59·9	+	51·4	51·1	—	59·5	58·7	+	98·8	95·6	—
83·8	82·6	—	35·3	35·1	—	20·6	20·8	+	51·1	51·3	—	76·8	78·6	+
56·7	57·6	+	73·9	74·1	+	42·0	41·9	—	49·5	48·7	—	43·4	41·5	—
61·8	59·6	—	27·8	27·6	—	75·2	75·4	+	47·2	47·4	+	44·8	46·8	+

The osmotic pressure of the cell sap is equivalent to that of a ·085 gram-molecular solution of sodium chloride, *i.e.*, is equal to 3·7 atmospheres.

Phyllocactus sp.

Gram-Molecular Concentration of NaCl.

·10			·09			·08			·07			·06		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
69·3	68·4	—	66·0	64·9	—	70·8	72·4	+	40·2	40·5	+	34·7	36·0	+
83·8	84·6	+	71·4	72·2	+	94·4	93·4	—	73·3	72·8	—	68·5	68·2	—
56·2	55·2	—	40·7	39·9	—	54·3	55·0	+	29·2	29·6	+	61·2	62·9	+

Therefore the osmotic pressure of the cell sap is equal to that of a ·085 molecular solution of sodium chloride, *i.e.*, to 3·7 atmospheres.

Cereus sp.

Gram-Molecular Concentration of NaCl.

·14			·13			·12			·11			·10		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
57·6	55·8	—	48·7	47·5	—	53·1	52·3	—	34·6	35·1	+	58·2	59·5	+
64·0	65·3	+	84·6	85·0	+	86·3	86·6	+	93·1	92·8	—	75·0	74·4	—
36·3	35·1	—	91·7	91·1	—	66·1	65·3	—	53·7	53·9	+	62·3	63·3	+
51·3	52·3	+	63·2	63·7	+	74·0	74·3	+	52·0	51·3	—	52·5	51·5	—
33·0	31·7	—	59·7	59·6	—	63·5	63·0	—	20·7	21·2	+	43·0	43·4	+

Osmotic pressure of cell sap taken to be same as that of a ·115 molecular solution of sodium chloride, *i.e.*, to be 5 atmospheres.

Crassula lactea.

Gram-Molecular Concentration of NaCl.

·09			·08			·07			·06			·05		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
65·7	64·2	—	33·0	32·7	—	59·4	57·5	—	75·9	76·6	+	37·5	37·9	+
55·9	56·9	+	55·2	55·4	+	82·0	83·2	+	63·3	61·7	—	57·6	56·9	—
74·4	72·9	—	60·8	61·3	—	53·2	51·3	—	57·7	60·0	+	60·8	61·1	+

Osmotic pressure of sap equals that of a ·065 molecular solution of sodium chloride, *i.e.*, is equal to 2·9 atmospheres.

On examining these results it will be seen that there is a considerable range of pressures obtained for the different plants. The osmotic pressure of a plant of *Salicornia ramosissima* from the

high ground of the marsh was found to be much greater than that of a plant from a depression on the marsh. The same values had previously been obtained by plasmolysis of the epidermal cells; when some of the plants examined from the higher parts of the marsh were found to have a cell sap isotonic with that of a 1·45 gram-molecular solution of sodium chloride while many of those from the lower parts had cell sap isotonic with that of a 1·15 solution. These values are high but they lie between the limits subsequently observed by Fitting[1] who found that the cell sap of plants of *Salicornia herbacea* from a very damp and salt habitat had cell sap of an osmotic pressure greater than that of a 1-gram-molecular solution and less than that of a 2-gram-molecular solution.

The strength of the cell sap of *Cereus* sp. found by Barger's method is in accordance with that found by Livingston[2] for a species of *Cereus*. He determined the osmotic pressure of the sap in two ways:—(i) by finding the depression of the freezing point which gave a pressure equal to that of 5·5 atmospheres, and (ii) by observing the change in curvature of "strips" of tissue placed in salt solutions of various strengths, when the pressure was found to vary from 3·9 to 7 atmospheres in different plants.

The values obtained for the other plants are somewhat lower than those generally expected for plant cells, but they are not so low as some recorded for other succulents. Cavara[3] estimates the osmotic pressure of the sap of *Aloë arborescens* to be equal to a pressure of 1·5 atmospheres.

The advantages which Barger's method has over other physical methods that have been tried for finding the osmotic pressure of the sap in plant cells, are twofold. In the first place a very small quantity of sap is sufficient to make a determination, so that the osmotic pressure of the cell sap of any small part of a plant, *e.g.*, a single leaf, can be estimated. This is necessary when it is desired to correlate the osmotic pressure of the cell sap of leaves, with age of leaf as done by Pringsheim[4] for certain succulent plants, or with any special factor in the life of the plant. The juice of the organ can be squeezed out by pressure of the fingers and the drops obtained can be used directly to fill the tubes. In the second place

[1] "Die Wasserversorgung und die osmotischen Druckverhältnisse der Wustenpflanzen." Zeitschr. f. Bot., Band 3, 1911, p. 250.

[2] "The Relation of Desert Plants to Soil Moisture and to Evaporation." Carnegie Institute, Publication No. 50, 1906.

[3] Loc. cit.

[4] "Wasserbewegung und Turgorregulation in welkenden Pflanzen." Jahrb. f. wiss. Bot., Bd. 43, 1896, pp. 89-144.

no elaborate apparatus is required,—the capillary tubes can easily be made by drawing out ordinary glass tubing.

There are, however, some disadvantages which must be considered. Firstly, the amount of time, which must be allowed to elapse between the two readings, is long. This is due to the low vapour pressure of water, the solvent used. It was generally found necessary to leave the tubes overnight to obtain a definite result. However, this length of time can be shortened by raising the temperature at which the drops are kept in the manner described by Barger and Ewins.[1] Secondly, the tubes require to be filled with great care, as the drops of the salt solution and of the cell-sap must not be allowed to mix on the sides of the tubes more than is unavoidable, a slight mixing being of course inevitable. With a little practice the tubes can be filled quite easily.

There is still another disadvantage which Barger's method has in common with the cryoscopic method and all others that deal with sap outside the cell. This is, it does not allow for any chemical changes that may take place and which might alter the osmotic strength of the sap. For this reason, Fitting[2] comments unfavourably on the use of the cryoscopic method. While working on *Salicornia* I estimated the osmotic pressure of the sap by plasmolysis and by Barger's method, and found that the results obtained in both cases varied between similar limits.

I wish here to express warm thanks to Professor F. W. Oliver, in whose laboratories part of this work was done, and to Miss E. N. Thomas for her kindness in reading and criticising the manuscript of this paper.

[1] "Application of the Microscopic Method of Molecular Weight Determination to Solvents of High Boiling Point." Trans. Chem. Soc., Vol. 87, 1905, p. 1757.

[2] Loc. cit., p. 223.

RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

BY F. CAVERS.

(Continued from p. 123).

FROM simple Cryptomonads—like *Protochrysis*, *Cryptochrysis*, or *Wysotzkia*—various diverging lines may be traced. One of these leads to the endozoic "Zooxanthella" forms; some at any rate of the "Zooxanthellæ" belong to the Cryptomonads and are placed by Pascher in a new genus, *Chrysidella*. Two other lines, marked by the fixation of the blue-green and the red chromatophores found sporadically in the simpler Cryptomonads, lead respectively to the blue-green genera *Chroomonas* and *Cyanomonas* and to the red genus *Rhodomonas*. Another line leads to *Cryptomonas* and *Nephroselmis*, with firm periplast, and from these have been derived the colourless forms *Chilomonas*, *Cyathomonas*, and *Oxyrrhis*. The fifth line has probably led to the Dinoflagellata (Peridiniales) on one hand, and through simple palmelloid types to the Phæocapsaceæ on the other. In the Phæocapsaceæ, beginning with simple gelatinous forms like *Phæoplax*, *Phæocystis*, and *Phæococcus*, we have a series of transitional types leading to the definitely filamentous *Phæothamnion* and so to the Ectocarpales.

The inter-relationships of the Brown Flagellate and Algal groups as here suggested are indicated on the accompanying scheme (Table C).

VIII.—THE PERIDINIALES (DINOFLAGELLATA) AND THEIR RELATIONSHIPS.

The Peridiniales, mainly marine but also found in fresh waters, and often forming a considerable part of the microplankton, are always unicellular and usually isolated, though sometimes cohering in chain-like colonies and in one family (Phytodiniaceæ) forming palmelloid aggregations by repeated division within gelatinous envelopes. There are typically two dissimilar flagella, usually lodged in grooves—one longitudinal and the other transverse—and in most cases the protoplasm is clad by a cellulose wall, typically built up of a series of sculptured and perforated plates. Oil is usually formed as the product of anabolism, even in forms possessing pyrenoid-like bodies, but in a few cases starch is produced. Most of the Peridiniales have yellow or brown or (in some freshwater species) green chromatophores, usually numerous and band or rod-like and radially arranged, but sometimes these are absent or represented by leucoplasts—these colourless forms are mostly saprophytic or in some cases holozoic, while Dogiel (41) and Chatton (21, 22) have recently shown that certain forms are

parasitic on various animals. Reproduction takes place by division into two or more daughter cells (spores or zoogonidia) and resting cysts are also formed by rejuvenescence of the cell contents. However, the life cycle of very few forms has yet been worked out,

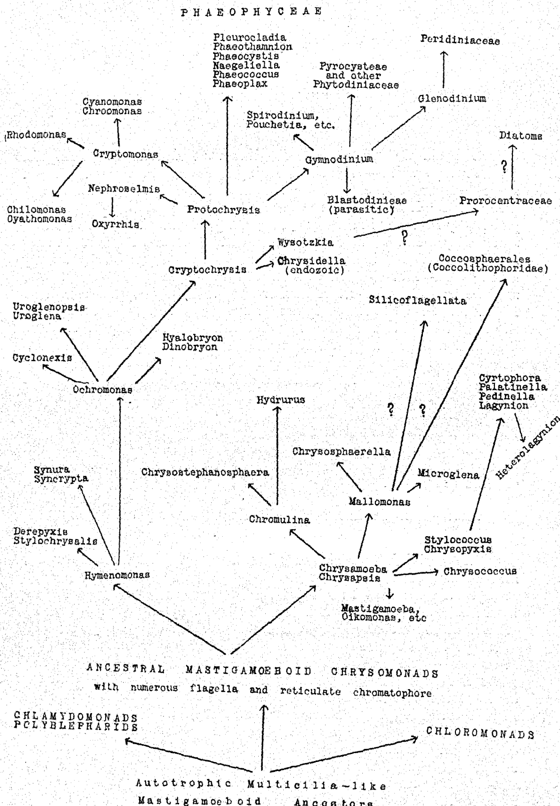


Table C.—Suggested Phylogeny of Brown Flagellate and Brown Algal Series. For details see Text.

despite the voluminous literature that has accumulated as the result of the collection of plankton Peridiniales, at all times of the year, by numerous workers; there is, for instance, no proof at present that a sexual process occurs in the group—unless we include in it the genus *Noctiluca* (see below). Zederbauer (157) observed individuals of *Ceratium Hirundinella*, a freshwater species, grouped in pairs and connected by protoplasm, while the contents of other individuals had been extruded in the form of a cyst—whence he inferred that zygospores had been formed as the result of a conjugation process. However, Jollos (62) and Wesenberg-Lund (145) observed the formation of similar cysts in *Ceratium* which had certainly arisen without copulation, and it would appear that the paired cells seen by Zederbauer had arisen as the result of abnormal cell division or that the process may be simply one of plastogamic fusion such as occurs in certain Protozoa.

Schütt (134) divided the Peridiniales into three families—Gymnodiniaceæ, Prorocentraceæ, and Peridiniaceæ. In the Gymnodiniaceæ the cell is naked or clad only by a thin mucilaginous or cellulose wall showing uniform structure and in most cases forming merely a delicate periplast like that of the majority of Flagellata. Of the two flagella, one is directed backwards in the longitudinal groove (sulcus) while the other (usually thrown into undulating curves) lies in the transverse groove (annulus). Both sulcus and annulus may be straight, meeting at right angles at one point where the flagella arise—in this case the annulus is either subequatorial (complete in *Gymnodinium*, a half-ring in *Hemidinium*) or is near the anterior pole so that the anterior (præ-annular) portion of the cell is much smaller than the posterior and is rostrum-like (*Amphidinium*); or the annulus may be spirally coiled and the sulcus slightly (*Spirodinium*) or markedly (*Cochlodinium*, *Pouchetia*) spiral also, meeting the annulus at both ends, with the transverse flagellum inserted at the anterior end of the annulus and the longitudinal flagellum at the posterior end of the sulcus—*Pouchetia* is distinguished from *Cochlodinium* by having a complicated stigmatic apparatus consisting of a red or black pigmented body with one or more large spheroidal refractive lens-like bodies adjoining it. In this family Schütt includes *Pyrocystis* (see below).

In the Prorocentraceæ (Fig. 8) there is a shell consisting of two biconvex valves, dotted with pores except on either side of the suture; from an opening in this suture, at the anterior end of the cell, arise the flagella, of which one is directed forwards while the second either vibrates about the base of the first or is directed laterally. In the three genera included here by Schütt, there are usually two large plate-like chromatophores, one lying within each valve of the wall, but sometimes these are deeply lobed or even divided into a number of radiating elongated chromatophores, as in the majority of Peridiniales. In *Cenchridium* the pore from which the flagella arise is continued inwards as a gullet-like tube; in *Exuviæella* and, more markedly, in *Prorocentrum*, there are small projections of the wall close to the flagellum pore, which Schütt suggests may represent the beginnings of the characteristic wing-like expansions of the margins of the flagellum groove in the Peridiniaceæ.

The remaining Peridiniales are placed by Schütt in the family Peridiniaceæ, in which the shell differs from that of the Prorocentraceæ in having a series of girdle plates intercalated between the two valves. The girdle consists essentially of a narrow ring-like plate with a groove (annulus) for the transverse flagellum, and a pair of plates (sometimes each divided into several plates) placed at right angles to this and containing the longitudinal groove (sulcus). Each valve consists of two or more polar plates, which are either joined directly to the girdle series or are separated by intercalary

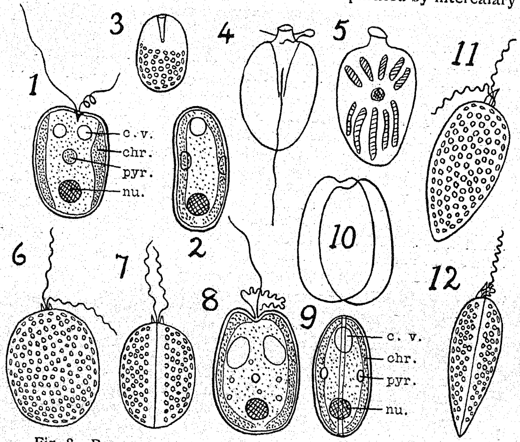


Fig. 8. Prorocentraceæ.—1, 2, *Haplodinium antjoliense* Klebs : 1, surface view ; 2, side view ; 3, *Cenchridium globosum* (Williams) Stein. 4, 5, *Amphidinium operculatum* Clap. et Lach. ; 4, ventral view, showing the flagella ; 5, dorsal view, showing nucleus and chromatophores. 6 to 10, *Exuviælla marina* Cienk. : 6 and 7, two aspects at right angles to each other, showing the flagella and the surface markings of the shell ; 8 and 9, optical sections corresponding respectively with 6 and 7, and showing the nucleus, chromatophores, pyrenoids, and contractile vacuoles ; 10, empty valves of the shell, after escape of encysted contents. 11 and 12, *Prorocentrum micans* Ehrb., two views at right angles. *Chr.*, chromatophore ; *c. v.*, contractile vacuole ; *nu.*, nucleus ; *pyr.*, pyrenoid.

1, 2, 8, 9, 10, from Klebs ; 3, 4, 5, from Stein ; 6, 7, 11, 12, from Schütt. All somewhat diagrammatic.

plates. The upper valve (epitheca) bears an apical pore, and in most cases the sulcus is confined to the lower valve (hypotheca), though sometimes it extends beyond the annulus right to the apex of the cell (*Steiniella, Gonyaulax*), or it may be short and extend equidistantly on either side of the annulus (*Protoceratium*). Schütt divides the Peridiniaceæ into four sub-families—Glenodinieæ (only genus *Glenodinium*); Ptychodisceæ (only genus *Ptychodiscus*); Dinophyseæ (six genera, including the most bizarre forms of

Peridiniales); and Ceratieæ (*Ceratium*, *Peridinium*, etc.—this is the largest division of the group). In the Dinophyseæ the shell is divided by a longitudinal suture into two subequal lateral portions the epitheca is much smaller than the hypotheca, the borders of the annulus are funnel-like and the left-hand border of the sulcus is often developed into wings and spines.

According to Schütt, the Peridiniaceæ are connected with the Gymnodiniaceæ by the genus *Glenodinium*, and with the Prorocentraceæ by the genus *Ptychodiscus*. In *Glenodinium* (Fig. 9, *9* to *13*) the shell is thin and structureless (not sculptured or perforated), and its differentiation into two valves and a girdle is only apparent when rupture occurs at liberation of the encysted contents. In *Ptychodiscus* the two valves have the same structure as in the Prorocentraceæ, but the girdle is represented by a thin soft membranous ring-like band, while the sulcus is indicated by a depression on one valve and a narrow plate on the other.

The results of recent work suggest considerable modifications of Schütt's classification of the Peridiniales, and appear to afford a basis for phylogenetic interpretations very different from those put forward by that author in 1896. Our knowledge of the Peridiniales and allied groups has been greatly extended in recent years by the work of Apstein (1, 2), Borgert (13), Chatton (21, 22), Dogiel (41), Jollos (62), Klebs (68), Kofoid (71, 72), Lemmermann (75–85), Lohmann (86-88), Schilling (127, 128), and others; the literature is cited by Pavillard (115) and in various other general works.

The view that the Peridiniales are related to the Flagellata appears to have been first put forward by Bergh (4), who pointed out the striking resemblances between *Prorocentrum* and the Cryptomonads. Bergh also suggested that a form like *Prorocentrum* might have given rise to the Dinophyseæ, in which the transverse groove is near the anterior end of the cell, and that the Ceratieæ are derived from the Dinophyseæ by progressive shifting backwards of this groove to an approximately median position. Bütschli (18), on the other hand, considered that in the evolution of the Peridiniales shifting of the annulus had taken place from behind forwards; according to his interpretation of the structure of *Prorocentrum*, which is followed by Schütt, the suture between the two valves is horizontal, and the insertion of the flagella lateral. Bergh and Bütschli agreed in regarding the simple shell-less Gymnodiniaceæ as derived by reduction from the typical shell-clad Peridiniales, and various other writers have adopted this view, as being a necessary consequence of the principle that the Peridiniales are of monophyletic origin.

A much simpler interpretation is obtained if we regard the suture in the Prorocentraceæ as being *longitudinal* and as corresponding with the longitudinal suture in the Dinophyseæ, which ought perhaps to be separated as a distinct family—the higher Peridiniales (Schütt's Peridiniaceæ) would then fall into two families, Ceratiaceæ and Dinophysidaceæ. Including the two families recently founded by Klebs and by Chatton, the Peridiniales as a whole may be regarded as forming two distinct series, which it is here suggested are of independent origin from the Cryptomonads.

The Gymnodiniaceæ (Fig. 9) may well have arisen from a Cryptomonad like *Protochrysis*, with two unequal flagella arising from a lateral depression having the form of an incomplete transverse groove. In the Gymnodiniaceæ, however, there are numerous chromatophores instead of two, and the nucleus, as pointed out by Klebs (68) has a characteristic fibrillar structure apparently not found in the Chrysomonadineæ. But granting these differences, and the absence of what may be strictly regarded as transitional

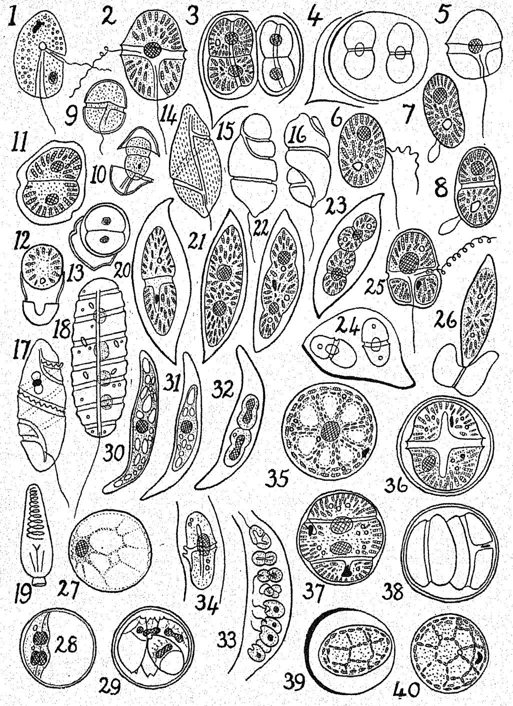


Fig. 9. Gymnodiniaceæ.—1, *Hemidinium nasutum* Stein, showing flagellum grooves, flagella, nucleus, and numerous small chromatophores. 2, *Gymnodinium bogoriense* Klebs. 3 to 8, *Gymnodinium rotundatum* Klebs: 1, two cysts enclosed in the membrane of the parent cell; 2, rupture of cyst shown on the left in preceding figure, to set free the two motile cells; 5, motile cell; 6, the

same gradually coming to rest and about to lose its flagella; 7, the same after loss of flagella, secreting a drop of mucilage for attachment; 8, the same, two days later (the transverse furrow which had disappeared on coming to rest has now been re-formed). 9, 10, *Glenodinium pulvisculus* Ehrb.: in 10 one of the shell-valves has been forced off to allow escape of the spore, which soon afterwards undergoes division. 11 to 13, *Glenodinium emarginatum* Klebs: in 11 the cell contents have undergone oblique longitudinal division; 12 shows escape of contents as a spore (cyst), and 13 the division of this cyst. 14, *Spirodinium spirale* (Bergh) Schütt. 15, 16, *Cochlodinium strangulatum* Schütt. 17, *Pouchetia fusus* Schütt, showing the spirally coiled flagellum grooves, and the stigma (consisting of a pigment-body with a refractive lens-like body on either side of it. 18, 19, *Polykrikos auricularia* Bütschli: in 18 the longitudinal flagellum groove, eight transverse grooves, four nuclei, and five trichocysts; 19, a trichocyst. 20 to 26, *Cystodinium bataviense* Klebs: 20, cyst with Peridinean body; 21 to 23, stages in division of cyst contents into two cells, which escape by gelatinisation of one side of the cyst (seen in 24); 25, motile cell; 26, motile cell has become a cyst, set free by rupture of the cell-wall; the black fleck in 20, 22, and 25 is a stigma ("eye spot"). 27 to 34, *Diplodinium lunula* (Schütt) Klebs (= *Pyrocystis lunula* Schütt): 27, uninucleate primary cyst; 28, cyst with four nuclei, the cytoplasm not yet divided; 29, cyst with four cells, each about to divide again; 30, sickle-shaped secondary cyst; 31, contraction of contents of same; 32, 33, division of contents into motile *Gymnodinium*-like cells, of which one is shown more highly magnified in 34. 35 to 40, *Hypnodinium sphæricum* Klebs; 35, a cell in optical section, showing the central nucleus, the numerous small chromatophores in the peripheral and radiating portions of the cytoplasm, an "eye spot," and five orange-red oil drops; 36, cell with rounded off contents showing *Gymnodinium*-like grooves; 37, stage in division, showing two nuclei, two transverse grooves, and two "eye spots"; 37, division into two *Gymnodinium*-like cells completed; 39, 40, rupture of cyst, setting free the two daughter cells, which have now lost their grooves.

1, 9, 10, from Stein; 2 to 8, 11 to 13, 20 to 26, 35 to 40, from Klebs; 14 to 17, from Schütt; 18, 19, from Bergh.

forms, there appears to be little doubt that the discovery of *Protochrysis* has at any rate lessened the gap between the Cryptomonads and a simple Peridinean genus like *Hemidinium* with its incomplete transverse groove. From a form like *Hemidinium*, the transition is easy to *Gymnodinium* and to *Glenodinium* (which is best placed in the Gymnodiniaceæ and which forms a connecting link with the Ceratiaceæ). These simple Gymnodiniaceæ form a central group from which diverge lines leading in various directions. In *Spirodinium*, *Cochlodinium*, and *Pouchetia* the cell is elongated and the grooves spirally coiled, and the pigmented body (stigma) found in the simpler forms is accompanied in *Pouchetia* by one or more lens-like bodies. In *Pouchetia armata* (Dogiel, 41) the cell is provided with nettling organs (trichocysts) consisting of a conical capsule containing a coiled stinging thread. Nettling organs of this kind are also found in the remarkable naked holozoic genus *Polykrikos* (Bütschli, 18; Kofoid, 72), in which the elongated body has eight transverse grooves and a single straight longitudinal groove, and there are eight nuclei—according to Delage (37) these are meganuclei, accompanied by smaller nuclei (micronuclei) as in Ciliate Infusoria, and each transverse groove has a flagellum. From Kofoid's account of *Polykrikos*, it would appear that the apparently single cell is a colony of individuals arranged in a linear series, owing to incomplete separation after division; Dogiel (41) has described specimens with four transverse grooves and a single nucleus. *Polykrikos* may be definitely placed in the Gymnodiniaceæ, since the presence of nettling organs in *Pouchetia* connects it with *Cochlodinium* and *Spirodinium* and thus with the simpler genera

like *Gymnodinium*. Whether *Polykrikos* forms a link between the Peridiniales and the Ciliate Infusoria is, of course, an open question in the absence of further transitional types. It is possible that the genus *Erythropsis* (Hertwig, 57; Delage, 37; Pavillard, 114) affords such a transition; in this organism the irregularly sphericai body shows a longitudinal groove, a transverse groove with a wavy flagellum at the anterior end of the body, and a relatively thick contractile outgrowth at the posterior end, while there is a stigmatic apparatus comparable with that of *Pouchetia*. Hertwig regarded *Erythropsis* as an Infusorian allied to *Vorticella*; while Metchnikoff compared its appendage to the sucker of *Acineta* and placed the genus in the Suctorial Infusoria. It is probable that the resemblances to Infusoria presented by *Polykrikos* and *Erythropsis* are merely superficial or due to homoplasy; in any case, both genera appear to be directly related to the Gymnodiniaceæ.

The life cycle of the lower Gymnodiniaceæ, so far as known, is extremely simple. In some cases division occurs in the motile condition, but more usually after encystment, the cyst being covered by gelatinous envelopes or by a firm wall and its contents dividing into two or more cells. In *Cystodinium* (Fig. 9, *20-26*) the motile cells resemble *Gymnodinium* in structure, but on becoming encysted they acquire an elongated and horned form, the contents then become rounded off and dividing to produce two or four motile cells. In *Diplodinium* (Fig. 9, *27-34*) the life cycle is somewhat complicated, since the encysted cell divides to form sixteen secondary cysts, each of which gives rise to four, eight, or sixteen motile *Gymnodinium*-like cells; to this genus Klebs refers *Pyrocystis lunula* and certain species which had previously been placed in the genus *Gymnodinium*. Finally, *Hypnodinium* (Fig. 9, *35-40*) is known only in the resting stage; on becoming encysted, the protoplast shows *Gymnodinium*-like grooves and divides into two naked cells exactly like *Gymnodinium* but without flagella—on being set free by rupture of the cyst these two cells acquire a membrane and soon form new cysts.

In the genera *Blastodinium* and *Apodinium*, recently discovered by Chatton (21, 22), and perhaps best placed in a family (Blastodiniaceæ) distinct from but closely allied to the Gymnodiniaceæ, which live as parasites or commensals in the bodies of Copepods and other marine animals, the cell divides into two portions, of which one continues the ordinary vegetative cycle while the other divides into a number of cysts which are set free as biflagellate *Gymnodinium*-like cells.

The genus *Diplodinium* leads from the Gymnodiniaceæ to the family Phytodiniaceæ (Fig. 10, *1-13*), which includes the old genus *Pyrocystis* (minus *P. lunula*, now transferred to the genus *Diplodinium*) and four new genera founded by Klebs (68). In this family the cells show Peridinean cytological features, though no grooves are present; reproduction takes place by simple division of the cell contents into two, but no motile cells have been observed. The simplest form is *Phytodinium*, with ovoid cells (Fig. 10, *1*, *2*); in *Pyrocystis* (Blackman, 8) the protoplasm is radially arranged, and is massed together at one end of the cell, very much as in the primary cyst of *Diplodinium lunula*; in *Tetradinium* (Fig. 10, *3-7*)

the cell is tetrahedral, with two pointed processes at each angle; in *Stylodinium* (Fig. 10, *8*, *9*) the oval or spherical cell is attached to a substratum by means of a gelatinous stalk; while in *Glœodinium*

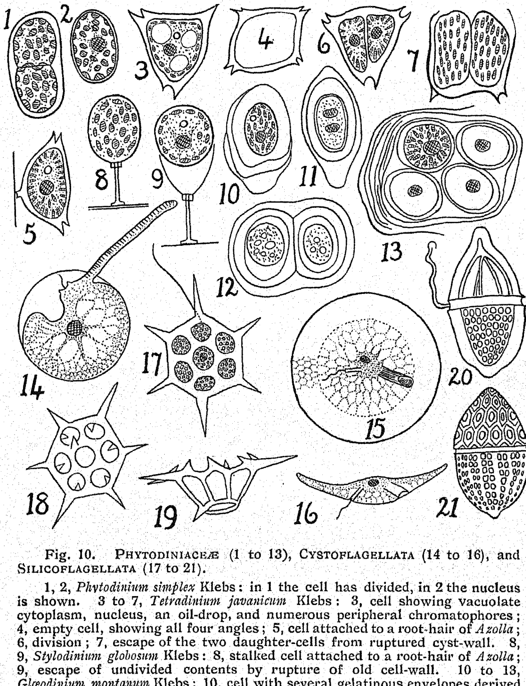


Fig. 10. PHYTODINIACEÆ (1 to 13), CYSTOFLAGELLATA (14 to 16), and SILICOFLAGELLATA (17 to 21).

1, 2, *Phytodinium simplex* Klebs: in 1 the cell has divided, in 2 the nucleus is shown. 3 to 7, *Tetradinium javanicum* Klebs: 3, cell showing vacuolate cytoplasm, nucleus, an oil-drop, and numerous peripheral chromatophores; 4, empty cell, showing all four angles; 5, cell attached to a root-hair of *Azolla*; 6, division; 7, escape of the two daughter-cells from ruptured cyst-wall. 8, 9, *Stylodinium globosum* Klebs: 8, stalked cell attached to a root-hair of *Azolla*; 9, escape of undivided contents by rupture of old cell-wall. 10 to 13, *Glœodinium montanum* Klebs: 10, cell with several gelatinous envelopes derived from older membranes; 11, division of the nucleus; 12, cell division; 13, older colony surrounded by gelatinous envelopes. 14, *Noctiluca miliaris* Suriray: side view (optical section), showing on the left the short flagellum inserted in the "pharynx," at the base of the thick tentacle. 15, 16, *Leptodiscus* Hertwig: 15, surface view, ventral side, showing on the right a wide depression with striated walls and on the left the narrow tube containing the flagellum; 16, side view (optical section). 17 to 19, *Distephanus speculum* Stöhr: 17, cell showing skeleton and cell-contents (nucleus, cytoplasm, chromatophores); 18, 19, two views of skeleton. 20, *Monaster rete* Schütt: side view, showing the two flagella arising from equatorial groove, and the internal skeleton. 21, *Amphitolus elegans* Schütt: side view, showing the elaborate skeleton.

1 to 13, from Klebs; 14 to 19, from Delage; 20, 21, from Schütt.

(Fig. 10, *10-13*), the most Alga-like form, colonies of considerable size are formed by repeated division within a thick stratified gelatinous investment.

The Noctilucaceæ (Cystoflagellata) are probably derived from *Pyrocystis*-like Peridiniales. In *Noctiluca* (Fig. 10, *14*) the spherical cell shows great resemblance in internal structure to *Pyrocystis*, though there is no cell-wall and there are, on the other hand, some elaborations not found in *Pyrocystis*—e.g., the thick tentacle which is transversely striated and shows movements, the short flagellum in the gullet-like opening guarded by two projections (" tooth " and " lip "). The reproduction of *Noctiluca* is a somewhat remarkable process—after conjugation of two cells budding occurs, and from the buds there arise motile cells which show *Gymnodinium*-like features—a transverse groove (without flagellum, however) and on the concave ventral side a backwardly directed longitudinal flagellum. The other genera of the family—*Leptodiscus* (Fig. 10, *15*, *16*) and *Craspedotella* (Kofoid, 71)—also show specialised structure, and do not serve to fill the gap between *Noctiluca* and *Pyrocystis*; in *Leptodiscus* the cell has the form of a watch-glass, the convex ventral surface having a wide gullet-like depression on one side, and on the other and a narrow pit containing a flagellum, while *Craspedotella* resembles a medusa in form.

Reference has already been made to a possible connection between Gymnodiniaceæ and the Infusoria. Certain organisms are also known which appear to lead from the Peridiniales to another group of Protozoa—the Radiolaria. The flagellated spores produced by various Radiolaria (for details and some of Brandt's figures of these, see Gamble's account of this group in Lankester's *Treatise on Zoology*, 151) present an extraordinarily close resemblance to *Gymnodinium* and other simple Peridiniales, and suggest the origin of this Protozoan group from *Gymnodininm*-like ancestors. Moreover, Schütt has described three genera which appear to form direct links between Gymnodiniaceæ and simple Radiolaria, and which also suggest the possible origin of the Diatoms; these genera (*Gymnaster*, *Monaster*, *Amphitolus*) have an internal skeleton which recalls that of Radiolaria, and the body is divided into two portions by an equatorial suture, which in *Amphitolus* (Fig. 10, *21*) and *Monaster* (Fig. 10, *20*) is grooved, while in *Monaster* the resemblance to Peridiniales is enhanced by the presence of two flagella inserted in this groove and springing laterally from the body. In addition, Borgert has shown that certain genera—*Distephanus* (Fig. 10, *17-19*), *Mesoscena*, *Dyctiocha*, *Cannopilus*—which had been previously placed in the Radiolaria (in the bodies of which they live as commensals, and with which they agree in having a siliceous skeleton) are Flagellate forms, for which he formed the group Silicoflagellata (see also Lemmermann, 80, 83); these organisms have a skeleton consisting of transverse rings which are either free or joined up by longitudinal spicules to form a network, and in the genera named there is a single flagellum (Borgert's new genus *Ebria* has two flagella), while the protoplasm contains numerous yellow chromatophores. The Silicoflagellata may have been derived from forms like *Monaster*, or they may have come from Chrysomonadinean ancestors—certain Chrysomonads

show a tendency to the formation of fi *Chrysosphærella*). The Coccosphærales 87) are perhaps derived from simple morphology they resemble forms like peculiar armour consisting of calcareo homogeneous perisarc and suggesting com lated siliceous armour of *Mallomonas*, though has been elucidated their affinities must rema

In connexion with the Cryptomonads, m of two remarkable and somewhat aberrant recently discovered by Scherffel,[1] the position scheme of classification above outlined appears to one of these forms, *Monomastix*, there are two large green chromatophores, each with a pyrenoid, and star the cell shows dorsiventral symmetry and there is a s flagellum. The other genus, *Pleuromastix*, is also a form, but has brown chromatophores and produces oil a also leucosin; it too has a single flagellum, inserted latera obliquely truncate anterior end of the body. Scherffel inc the view that *Monomastix* belongs to the Polyblepharidac Pascher (in reviewing Scherffel's paper in *Zeitschr. f. B* 1913, p. 405) considers that its affinities lie rather Cryptomonads; both writers refer *Pleuromastix*, somewha fully, to the Chrysomonads. The most remarkable cha common to these genera, apart from the possession of a sin flagellum (all hitherto described Cryptomonads and Chloromonads have two flagella, though one order of Chrysomonads, the Chromulinales, is characterised by a single flagellum) is the presence of peculiar structures somewhat resembling the trichocysts found in some Chloromonads (*Rhaphidomonas*, *Merotricha*) and Peridiniales (*Polykrikos*, see above) as well as in the Ciliate Infusoria. These trichocyst-like organs, especially well developed in the green form *Monomastix*, consist of a highly refractive outer layer and a less refractive central mass which on treatment with various reagents is protruded rapidly as a filament (in *Pleuromastix* usually as a distinctly tubular structure). According to Scherffel, the structure of these organs in the two new Flagellates confirms the suggestion put forward by Künstler that the peculiar granular organs found lining the gullet-like depression in the Cryptomonad body represent rudimentary trichocysts. Among the Ciliate Infusoria corresponding organs occur, in addition to more highly organised trichocysts, and it appears probable that in both cases structures of this kind are not always to be regarded as defensive organs but may be merely products of secretion. Apart from its possession of pyrenoids and starch, *Monomastix* might well be placed in the Chloromonads, but on the whole it would appear that both genera may be perhaps best classed provisionally among the Cryptomonads—as here treated, this is a somewhat varied and generalised one, with many divergent affinities.

[1] "Zwei neue trichocystenartige Bildungen führende Flagellaten." Arch. f. Protistenk., Bd. 27, 1912, pp. 94-128.

(*To be continued*).

(Fig. 10, *10-13*), the most A[illegible] size are formed by repea[illegible] gelatinous investment.

The Noctilucaceæ ([illegible] *Pyrocystis*-like Peridini[illegible] cell shows great rese[illegible] though there is no ce[illegible] elaborations not fou[illegible] is transversely stria[illegible] in the gullet-like o[illegible] "lip"). The rep[illegible] process—after c[illegible] the buds ther[illegible] features—a t[illegible] the concav[illegible] flagellum. T[illegible] *15, 16*) an[illegible] structure[illegible] *Pyrocyst*[illegible] the c[illegible] one si[illegible] while *Cra*[illegible]

Re[illegible] betwe[illegible] are[illegible]

RECENT LITERATURE.

[illegible]CT ANTARCTIC FLORA.

[illegible]orst[1] published a preliminary note on a [illegible]ssic plants obtained by Dr. J. G. Andersson in [illegible] 57° W., in the course of a visit to Graham [illegible]öld's Swedish Antarctic Expedition (1901-3). [illegible]wn to the close resemblance of the plants as a [illegible]e Jurassic Flora of East Yorkshire. A detailed [illegible]e Graham Land plants has now been published by [illegible][2], to whom Prof. Nathorst entrusted the work of [illegible]ese exceptionally interesting palæobotanical records. [illegible]derson's discovery of the Jurassic flora, Capt. Larsen [illegible]d some pieces of petrified wood on Seymour Island [illegible] S.), and from this locality the Swedish expedition [illegible]several Tertiary plants and a single coniferous twig of [illegible]ous age resembling *Sequoia fastigiata* (Sternb.). The [illegible]y plants were described by Dusén in 1908[3], and an account [illegible]he coniferous woods has been published by Dr. Gothan[4]. [illegible]s of Sir Ernest Shackleton's expedition found some fossil [illegible]d recorded the occurrence of a seam of coal in lat. 85° S.

[illegible]raham Land plants were collected at Hope Bay in a dark [illegible] rock, capped by volcanic tuffs, which also afforded a few [illegible]perfectly preserved bivalves believed to be freshwater species.

Dr. Halle prefaces the descriptive part of his paper by some interesting remarks on the principles of classification or nomenclature of fossil plants, and states that he has "acted on the conviction that it is a lesser evil to keep forms separated which are identical than to identify such as are distinct." It is, on the other hand, arguable that as it is a sound general principle "to keep the mind open when there is no sufficient warrant for closing it"; so in the case of fossils, if there are no satisfactory reasons for separating forms which bear a close resemblance to one another, it is wiser to use specific names in a liberal sense. The real difficulty is that in dealing with more or less fragmentary remains of vegetative organs we lack adequate data on which to base conclusions as to the range of specific variation, and whatever guiding principle is adopted the student cannot as a rule achieve more than a provisional result. In one of his letters Darwin describes, in terms which will appeal to all who have attempted to determine impressions of fossil plants, the state of mind induced by his systematic work on Cirripedes—"After describing a set of forms as distinct species, tearing up my MS. and making them one species, tearing that up and making them separate, and then

[1] Compt. Rend., June 6th, 1904.

[2] "The Mesozoic Flora of Graham Island." Wiss. Ergebnisse der Schwedischen Südpolar-Expedition, 1901-1903. Bd. III, Lief. 14, Stockholm, 1913.

[3] "Ueber die Tertiäre Flora der Seymour-Insel." Ibid., Bd. III, Lief. 3, 1908.

[4] "Die fossiler Hölzer von der Seymour-Insel." Ibid., Bd. III, Lief. 8, 1908.

making them one again, I have gnashed my teeth, cursed species, and asked what sin I had committed to be so punished."

Halle writes in defence of his position—"Only, if the species are narrowly delimited, the eventually established relation between the floras will be much more reliable than if the opposite principle is adopted." This statement implies that the slight differences on which specific separation is based are something more than the expression of the plant's plasticity, and hardly takes sufficient account of the lessons taught by the vegetative organs of recent plants.

But these are questions of secondary importance, and in all systematic accounts of fossil floras the personal bias of the author must be the determining factor.

Dr. Halle's work is characterised by thoroughness and accuracy, and whether or not one may agree with all his determinations, his descriptions and illustrations are a substantial contribution of considerable value. The Equisetales are represented by a single species hardly distinguishable from the Indian Jurassic type *Equisetites rajmahalensis* Schimp. but referred by Halle to *E. approximatus*, a designation previously suggested by Nathorst. The widely spread Jurassic species *Sagenopteris Phillipsi* (Brongn.), for which Halle adopts the unfamiliar but older name *S. paucifolia* (Phill.), is represented by some well-preserved leaflets. Ferns are abundant, though unfortunately nearly all the specimens are sterile. The characteristic Middle Jurassic type *Todites Williamsoni* (Brongn.) occurs in both a sterile and fertile state, and some fertile pinnæ are described under the name *Coniopteris* cf. *nephrocarpa* (Bunb.), though the Yorkshire specimens on which Bunbury founded his species *Sphenopteris nephrocarpa* are usually regarded as indistinguishable from the protean type *Coniopteris hymenophylloides* (Brongn.), also recorded from Graham Land. The genera *Cladophlebis* and *Sphenopteris* appear under various forms; several new specific names are instituted, and in some cases on evidence which is hardly convincing. *Dictyophyllum* and sterile pinnæ probably, as Halle believes, identical with *Klukia exilis* (Phill.) afford other familiar instances of cosmopolitan Jurassic plants. Saporta's genus *Scleropteris* is revived for specimens similar to the European species *S. Pomelii* Sap. *S. furcata* Halle is described as characterised by the forking of the rachis, a feature which suggests comparison with Zigno's Italian species of *Dichopteris*, a genus omitted by Halle in his discussion of the characters of *Scleropteris* and *Pachypteris* though there would seem to be no adequate reason for discarding *Dichopteris* in favour of *Scleropteris*[1]. The difficulty of drawing a line between *Pachypteris* and *Thinnfeldia* is considered, and under the former name is included *P. dalmatica* Kern., a form to some extent transitional between *Thinnfeldia* and *Dichopteris*, which might reasonably be included in the latter genus.

Cycadean fronds form a conspicuous feature in the Hope Bay flora, including examples assigned to *Nilssonia*, *Pseudoctenis*, *Zamites*, *Otozamites*, *Ptilophyllum*, and a small specimen which may, as Halle suggests, belong to a *Williamsonia*. The generic name

[1] Seward, "Fossil Plants," Vol. II, p. 552.

Zamites is used for several forms which agree much more closely with *Ptilophyllum* fronds than with *Zamites* as usually employed. Conifers are represented almost entirely by vegetative shoots, but the presence of Araucarian cone-scales of the *Eutacta* type is a feature of special interest; the seed-bearing scales are referred to Feistmantel's Indian species *Araucarites cutchensis*, but, as Halle points out, they also agree very closely with the English Jurassic species *A. Brodiei* Carr., not to mention other examples from South Africa, Scotland, and North America. Halle institutes a new genus *Elatocladus* for "sterile Coniferous branches of the radial or dorsiventral type, which do not show any characters that permit them to be included in one of the genera instituted for more peculiar forms." It is unfortunate that most of the generic names applied to fossil Coniferous shoots are based to a large extent on the cones, and these are frequently not preserved or occur apart from the vegetative branches. The nomenclature certainly needs revision. An objection to Halle's generic term as he defines it, and one which is recognised by him as a possible drawback to its extended application, is that it includes forms with leaves of the *Taxites* type as well as branches with leaves like those of *Sphenolepidium*, *Elatides*, and other genera. An alternative plan is to retain *Taxites* in the wide sense in which it is used by most authors for twigs bearing linear and usually distichous leaves similar to those of *Taxus*, certain species of *Podocarpus*, *Sequoia sempervirens*, and other recent Conifers, and to adopt the name *Pagiophyllum*, for forms with radially disposed leaves like those of *Elatides*, *Sphenolepidium*, and *Cheirolepis*. A species of *Elatocladus* instituted by Halle (*E. heterophylla*) affords an interesting example of dimorphic foliage which might well be compared with shoots of some recent species of the southern hemisphere genera *Dacrydium* and *Podocarpus*.

There can be no doubt that, as Halle says, the Graham Land plants are relics of a Jurassic flora, though some of them are identified, and no doubt correctly identified, with Wealden species. Although there are some common Jurassic types which have not as yet been recorded from this Antarctic region, notably *Ginkgo*, *Baiera*, *Phœnicopsis*, *Czekanowskia*, and others, the occurrence of several ferns and gymnosperms specifically identical with Arctic, North European, North American, and Asiatic Jurassic plants is a remarkable testimony to the world-wide distribution of a Mesozoic flora. The phytogeographical and climatological problems emphasized by this most recent contribution to Mesozoic Botany have not received the attention they deserve, and for this as for other reasons Dr. Halle's critical work is especially welcome.

The correlation of the Graham Land flora with that of East Yorkshire or with some of the Upper Gondwana floras of India cannot be regarded as necessarily carrying with it the implication that species common to Arctic, Antarctic, and other regions were in existence at the same time. As Huxley wrote, "There seems, then, no escape from the admission that neither physical geography nor palæontology possesses any method by which the absolute synchronism of two strata can be demonstrated."

A. C SEWARD.

LABORATORY NOTES.

SOME SIMPLE PHYSIOLOGICAL DEMONSTRATIONS.

BY

F. E. FRITSCH, D.Sc., PH.D.,

Professor of Botany, East London College, University of London;

AND

E. J. SALISBURY, B.Sc.,

Lecturer in Botany, East London College, University of London.

[WITH ONE FIGURE IN THE TEXT].

IN connection with a course of lectures recently given by one of us, a number of simple methods of physiological demonstration have been worked out, some of which seem to us to be of sufficient interest to warrant a brief description.

1. *An artificial stoma.*—Diverse models of stomata constructed of unequally thickened rubber are described by various authorities, but none of these are easily made, the materials are somewhat costly, and moreover, the results are not always satisfactory. The artificial stoma about to be described, though open to certain objections, has the great advantage over rubber-models that it can be made at any time and in the space of a few minutes. To construct such a model the stem of an herbaceous plant provides all the material that is required. We have found the scape of a jonquil, Narcissus or daffodil, and particularly the internode of the dog's mercury (*Mercurialis perennis*) to be perfectly satisfactory; the petiole of the cuckoo-pint (*Arum maculatum*) and the internode of the dead-nettle also furnish suitable material. A straight piece about three to four inches long (in the case of the dead-nettle one to two inches long) is selected and is halved lengthwise. The two halves thus obtained are then placed in strong salt solution until they become flaccid. They are thereupon placed parallel to one another in such a way that the original outer surfaces of the internode or scape are in juxtaposition, while what was previously the inner surface faces outwards. In this position the two halves are firmly tied together by string at their two ends (Fig. 1, B, *a*). If the two pieces thus joined together are placed in tap water, in the space of a few minutes they will (as they gain in turgescence) arch apart so as to leave a wide aperture between them (cf. Fig. 1, B, *b*) —in other words the pore of the artificial stoma opens. A return to the salt solution again results in the closure of the pore, and this sequence of events can be repeated several times. If the artificial stoma with the pore widely open is allowed to dry slowly by exposure to the air, a marked decrease in the width of the opening becomes manifest after some time, although the closure is not so complete as when due to plasmolysis.

The advantages of this model lie in the fact that it demonstrates the influence of changes of turgescence in leading to the opening and closing of the pore, and that the inner faces of our model guard cells consist of thicker material than the outer. On the other hand we are of course dealing with cell-complexes in place of cell-units, but as the method is intended only to demonstrate to a class the mode of action of the stomatal mechanism, this does not seem to us to be a vital objection.

2. *Continuity of the aërating system of the plant.*—The ordinary wash-bottle method[1] of illustrating this important fact depends entirely on obtaining a suitable leaf, and has the further drawback that it is not readily demonstrated to a class. By utilising an air-pump the continuity of air-spaces in the plant is of course readily shown, but the method about to be described only involves the use of materials that are to be found in any laboratory, and moreover, operates for some considerable length of time without attention. For the purpose of this experiment we use a round-bottomed flask, provided with a rubber cork, through a single hole in which a piece of glass tubing twice bent at right angles is inserted (Fig. 1, A). The one arm of the glass tube projects only for a short distance below the cork, while the other (free) arm is considerably longer. To the open end of the latter a branch bearing leaves or a single leaf is fitted by rubber tubing so as to make an air-tight connection, the cut end of the stem or petiole extending into the tube above the level of the surrounding rubber (cf. Fig. 1, A, *a*). Prior to doing this the long arm of the glass tube is partially filled with a column of water extending some four to six inches above the cut end of the stem or petiole (Fig. 1, A, *b*). The rubber cork with attached tubing is now taken out of the flask, and the latter is then half filled with water, which is heated until it has boiled for a minute or two. While the flask is still filled with water-vapour the rubber stopper is fitted into it, and the flask is placed in a vessel of cold water. The reduced pressure within the flask resulting from the condensation of the contained water-vapour leads to a strong suction, and as a result a stream of air-bubbles commences to arise from the cut end of the stem or petiole and to ascend through the column of water in the longer arm of the glass tube (cf. Fig. 1, A). This goes on for several hours, whilst the flask slowly cools. The stream of bubbles is so pronounced that the experiment is readily visible to a class of moderate size, whilst the result of the experiment, for demonstration to larger numbers, can easily be projected on to a screen by the aid of a lantern.

3. *Recovery of a flaccid shoot.*—The same apparatus can also be used to demonstrate the recovery of a flaccid shoot on being injected with water. For this purpose the upper end of the shoot is removed and the cut surface thus produced is attached as before to the long arm of the tube, whilst the lower end of the shoot is placed in a beaker of water. In order to prevent the entry of air into the tissues by way of the stomata both surfaces of the flaccid leaves should be vaselined. As a consequence the suction generated within the flask (as in the previous experiment) operates in causing a rapid flow of water through the shoot. After a little time the leaves become turgid.

[1] Detmer and Moor. "Practical Plant Physiology" (1909), p. 172, Fig. 61.

4. *Rate of flow of water through the wood.*—For the purpose of this experiment, as for others ordinarily requiring the use of an air-pump, the same method as described in the two previous cases can be employed. By a simple modification it can be adapted for comparative results. Thus, if the flask in Fig. 1, A, be fitted with a two-holed stopper, *each* hole bearing a piece of glass tubing like that shown in the figure, the rate of flow through two branches (*e.g.*, those of a Dicotyledon and a Conifer), subjected to identical amounts of negative pressure, can be compared. The upper cut

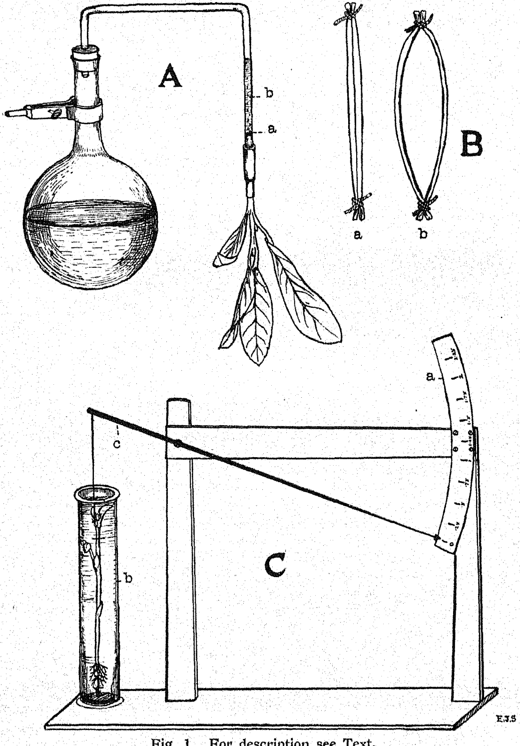


Fig. 1. For description see Text.

ends of the branches are fitted on to the free ends of the glass tubes with rubber tubing as before but without the column of water above, while their lower ends dip into beakers filled with water. The surface of the branches should previously be coated with a layer of paraffin wax so as to close up all apertures and scars. The relative conducting powers of the two branches will of course be proportional to the heights of the columns of water that form in the glass tubes above their cut ends.

5. *Demonstration of water-pores.*—We have adopted the same principle for the rapid demonstration of water-pores. To the longer arm of the tube is attached a glass cylinder supplied at both ends with rubber corks perforated by a single hole and sufficiently wide to accommodate the leafy portion of the branch to be experimented with. The branch is inserted through the hole[1] in the lower cork so that its foliage is situated within the glass cylinder, whilst the lower cut end of the branch projects below the cork into a beaker of water. Owing to the reduced pressure produced in the apparatus as before, a considerable quantity of water is sucked up into the shoot, and drops of moisture are soon formed over the water-pores. Branches of *Fuchsia* give a good result.

6. *Demonstration of the shrinkage of an herbaceous plant as the result of loss of turgescence.*—The importance of turgescence in maintaining the rigidity of an herbaceous plant is easily demonstrated by familiar methods, but a means of making the resulting shrinkage obvious to a whole class has not, as far as we are aware, been yet described. We use for this purpose a simple lever working over the surface of an arc, graduated to show the actual distance to which the movement of the long arm of the lever corresponds (Fig. 1, C). To the short arm of the lever (*c* in Fig. 1, C) an entire herbaceous plant is firmly tied by its apex, and to the other end of the plant is attached a weight sufficiently heavy (one to two pounds) to keep the plant in position at the base of the glass cylinder *b* (Fig. 1, C). The latter should be tall enough to include the whole plant. If necessary, sufficient weights can be attached to the long arm of the lever to keep the plant fully extended without undue strain. The cylinder is now carefully filled with strong salt solution and the position of the pointer on the graduated arc noted. After about half-an-hour the pointer on the arc will record a shrinkage of a quarter to half an inch according to the nature and size of the plant used in the experiment. If the salt solution is then siphoned off and replaced by water, the gradual recovery of the plant can be noted in the same way.

[1] An excellent method of fitting a branch into a rubber cork is described and figured by Osterhout, "Experiments with Plants," 1908, p. 205, Fig. 118.